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A CENTURY OF SCIENTIFIC PUBLICATIONS AT THE MISSOURI BOTANICAL GARDEN

The Missouri Botanical Garden, founded in 1859, originated as the country estate of St. Louis businessman Henry Shaw (1800–1889), who made the Garden and neighboring Tower Grove Park gifts to the city of St. Louis, Missouri. From the outset, the Garden was a center for horticultural display, education, and botanical research. The young institution jumped quickly to prominence in botanical research through Mr. Shaw's association with Dr. George Engelmann, an obstetrician and one of the leading botanists of the time. Dr. Engelmann took full advantage of the position of St. Louis as the Gateway to the American West by coordinating and participating in western botanical exploration. And to the east, he maintained correspondence with and passed specimens to Harvard botanist Asa Gray.

Botanical education followed closely on the heels of research. In 1885 Mr. Shaw established and endowed the Henry Shaw School of Botany at nearby Washington University. A rising star in the botanical world, Dr. William Trelease, previously at the University of Wisconsin, was selected to be Engelmann Professor of Botany in the new program.

When Henry Shaw died in 1889, his will placed the Garden in the hands of a Board of Trustees and a Director. The Board called upon the Director to publish an *Annual Report*. The first report, in 1890, contained a biographical sketch of Mr. Shaw, details of his will and related documents, a report from the Henry Shaw School of Botany, accounts of activities at the Garden, and the *First Annual Report* by the Director (who by 1890 was William Trelease).

The second *Annual Report* likewise contained the Director's Report and accounts of institutional activities, *and* there appeared the Garden's first scientific publication, "Revision of North American species of *Epilobium*," by W. Trelease. (Onagraceae have made frequent subsequent appearances in our scientific publications.) The next year's *Annual Report* held two scientific papers, including the classic "The yucca moth and yucca pollination" by Charles Riley. Following issues regularly contained multiple scientific papers from the Henry Shaw School of Botany and from outside contributors.

The subject matter was broad: physiology, taxonomy, phenology, pathology, economic botany, plant chemistry, soil science, limnology, and additional areas. Titles ranged from "An ecological cross section of the Mississippi River in the region of St. Louis" (1908) to "A consideration of the physiology and life history of a parasitic *Botrytis* on pepper and lettuce" (1912).

By 1912, the year of the *Twenty Third Annual Report*, it was clear that two publications were necessary to cope with the Garden's need for scientific and nonscientific outlets. Since then the

Bulletin of the Missouri Botanical Garden has been the vessel for accounts of Garden activities, popular articles, and annual reports from the Director. The *Annals of the Missouri Botanical Garden* was founded at essentially the same time for scientific articles. Volume 1 of the *Annals* came out in 1914 and contained 20 highly diverse articles, including one dealing with air pollution by bacteria in human breath.

Over the years, the focus of the scientific publications narrowed considerably, most notably with abandonment of bacteriological, physiological, and pathological material. There appeared an intensified focus on plant systematics and related subjects, including ecology at times. Emphasis has been tropical with special emphasis on Central America.

In 1937 Robert Woodson, Jr., and Russell Seibert published "Contributions toward a flora of Panama. I. Collections in the provinces of Chiriquí, Coclé, and Panamá," the first glimmer of *The Flora of Panama*, which became a dominant theme and formal series in the *Annals*. The *Flora* was launched by Dr. Woodson and R. W. Schery in 1943 and was concluded in 1981 by W. G. D'Arcy—6,818 printed pages and 5,314 species later. (For a history of the flora, a checklist, and an index by W. G. D'Arcy see *Monographs in Systematic Botany from the Missouri Botanical Garden*, Volume 17.)

A second major long-term subproject of the *Annals* began in 1969 with publication of the Garden's 16th Annual Systematics Symposium. A full history of annual symposium publications follows:

Symposium number	Volume (issue)	Year	Symposium
16	56(3)	1969	Tropical Island Biogeography
17	59(3)	1972	Hybridization, Evolution, and Systematics
[18, 19 not published]			
20	61(3)	1974	Plant–Animal Coevolution
21	62(2)	1975	Biogeography
22	63(2)	1976	Evolution at the Population Level
23	64(2)	1977	Chemosystematics
24	65(2)	1978	Systematic Studies in Africa
25	66(4)	1979	Palynology and Systematics
26	68(1)	1981	Evolution and Systematics of the Gramineae
27	68(2)	1981	Reproductive Strategies in Plants and Animals
28	69(3)	1982	Biological Studies in Central America
29	70(3)	1983	Biogeographical Relationships between Temperate Eastern Asia and Temperate Eastern North America
30	72(4)	1985	The Implications of Phylogenetic Analysis for Comparative Biology
31	73(3)	1986	Topics in North American Botany, A Symposium Commemorating George Engelmann
32	74(2)	1987	The Biology of Epiphytes
33	75(1)	1988	Species Diversity
34	75(4)	1988[1989]	Macromolecular Approaches to Phylogeny
35	77(1)	1990	Conserving Biological Diversity: Prospects for the 21st Century

Additional (unnumbered) symposium publications have been:

	59(2)	1972	Disjunctions in Plants
	61(1)	1974	25 Years of Botany
	61(2)	1974	Evolution of Systematic Characters in Ferns

Volume (issue)	Year	Symposium
62(3)	1975	The Bases of Angiosperm Phylogeny
64(4)	1977	Perspectives in Tropical Botany
71(1)	1984	The Evolution of Dioecy
71(3)	1984	The Order Myrtales
74(4)	1987	Contributions to a Symposium on the Evolution of the Modern Flora of the Northern Rocky Mountains
75(3)	1988	Reproductive Biology of Freshwater Aquatic Angiosperms
75(4)	1988	Rhizophoraceae–Anisophylleaceae
77(1)	1990	The Biological Diversity and Evolution of the Tarweeds

In 1983 a series of guides to plant collecting began. Published so far are guides to collecting bamboos (70-1), Pandanaceae (70-1), aquatic and marsh plants (71-1, 73-4), passionflowers (71-4), Araceae (72-2), palms (73-1), Lecythidaceae (74-2), botanical specimens (73-3), and Cyclanthaceae (74-4). Several additional contributions are in preparation.

By 1978 the need for a split in the scientific publications was satisfied by initiating *Monographs in Systematic Botany from the Missouri Botanical Garden* to accommodate works too large for the *Annals*. Monograph number 1 was *A Provisional Checklist of Species for Flora North America*. The second monograph was E. R. Eisendrath's *Missouri Wildflowers of the St. Louis Area*. The most recent addition to the series is number 31, Carlyle A. Luer's *Icones Pleurothallidinarum. VI. Systematics of* Pleurothallis—*Subgenus* Ancipitia *Subgenus* Scopula—*and* Trisetella.

As the first century of scientific publications ends, new challenges are emerging. How do we distribute our works to individuals when soaring publication costs force prices to levels only affordable by large institutions? What is the optimal role for computers in the publication process? As the Neotropics, featured for so long in our publications, are deforested and transformed culturally, where do we aim our view, and in what tones? However we answer these questions, we remain confident that systematic botany and related fields are expanding, diversifying, integrating, and surging forward in exciting new directions. Here lies the real challenge and joy of stepping into our second century.

—George K. Rogers,
Editor

THE REAL WORK OF SYSTEMATICS[1,2]

Michael E. Soulé[3]

ABSTRACT

Two recent revelations, that the number of species is much greater than previously thought, and that they are disappearing at a frightening rate, should impel systematists to question the implicit objectives of their discipline. It is impossible, using traditional methods, to describe and classify most species in the lesser-known groups. It is suggested that systematists and other organism-ecological biologists must collectively establish criteria for research priorities so that the "real work" of biology in the next few decades can be achieved. Research on many fronts is essential if we are to maintain a significant fraction of the planet's biodiversity.

Blessed is he who has found his work;
let him ask no other blessings.
—Thomas Carlyle, Past & Present,
Bk. III (1843)

WHENCE THE CLASSIFICATION PROJECT NOW?

Two recent revelations should impel a deep analysis of the premises on which systematics has operated. The first revelation is the discovery that 300 years or so of laborious taxonomic work has not brought civilization within 10% of the way to its goal of describing the biological world. This would be arresting even if it were not for the second revelation, which is that the planet is on the verge of an anthropogenic mass extinction that will annihilate much of its biotic diversity even before it can be cataloged.

These facts—the unsuspected vastness of biotic diversity and its current vulnerability—are a major challenge to the taxonomic enterprise, including its goal, its cultural role, and its methodologies. On the other hand, this is an opportunity for systematists to take stock and ask what is the real mission, the "real work" of systematics.

Almost 250 years ago, a great project to classify all life was systematized by the Swedish naturalist Linnaeus, who is considered the father of the modern binomial system of nomenclature. Living systematists are the proud carriers of that tradition. The project has accomplished a staggering amount of work. In all, over 1.4 million species have been described and classified, using time-tested, if inflexible, formulae.

Until recently, it was understood that this project was about half finished. Now we know differently. It is apparent that the biological world is richer than any of us could have imagined just a few decades ago. Recent investigations in the tropics (Erwin, 1988) have increased our estimates of the number of fellow species on this planet from a few million to tens of millions, mostly tropical arthropods. What are the implications of these hordes of undescribed species for systematics? Is this a marvelous challenge or a task of Olympian impossibility? Either way, the great Linnaean project has received a shocking setback—one that must, sooner or later, trigger a searching appraisal by those scientists who see it as their mission to classify and catalog all forms of life.

Of course, the problems are greater for some taxa than for others. For vertebrates, the classification project is certainly more than half done, although ichthyologists are naming some 250 new species of fish each year, most of them small, freshwater species. For a few popular groups—vascular plants, vertebrates except fishes, butterflies—the project may be within 10% of its goal (Peter Raven,

[1] This and the four articles that follow it are the proceedings of the 35th Annual Systematics Symposium of the Missouri Botanical Garden, *Conserving Biological Diversity: Prospects for the 21st Century*. The symposium was held 7–8 Oct. 1988 at the Missouri Botanical Garden in St. Louis, Missouri, U.S.A. The Annual Systematics Symposium is supported in part by a grant from the National Science Foundation. We gratefully acknowledge their continued support for the 34th year of this 35-year series.

[2] The title of the paper is borrowed in part from Gary Snyder's book, *The Real Work*. To Joel Cracraft, Paul Ehrlich, Peter Raven, and Warren H. Wagner I am grateful for much good advice, but, obviously, responsibility for these utterances is mine.

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pers. comm.), though formidable challenges remain. Many hundreds of plant species are being described each year. However, the taxonomic task assumes mind-boggling proportions for such taxa as arthropods, polychaetes, and nematodes.

Even before the scale of the recent revelations was apparent, Peter Raven (1977) wrote the following: "It is too late in the history of the world to think that there is time to produce ordered classifications of all plants, animals, fungi, and microorganisms, and then to employ these classifications to seek new kinds of generalities while these organisms are still extant."

Why is it too late? Let's take a quick look at the "extinction scenario," using plants as our example. Plants are numerous, their regional diversity is probably representative of other groups, and they are relatively well known taxonomically. About half of the 250,000 species of plants are associated with just 6–7% of the land surface—tropical forests. Most of these forests are likely to be destroyed or greatly disturbed during the next few decades. What kind of extinction scenario does this portend?

The paucity of information on the geographic extent (range) of most tropical species currently prevents us from estimating accurately the consequences of so much habitat destruction. Most of the current estimates assume that the density of protected areas (nature reserves) is too sparse to capture many locally endemic species. If this premise is wrong, and most tropical species are relatively widespread, extinction rates could be lower than most futurists predict, at least in the short run. A conservative estimate, I believe, would be that 25% of tropical plant species will be extinguished by the year 2020. In other words, we will see a loss of about 34,000 species of plants, 12.5% of the world's flora, within the next few decades. A much larger fraction of insect species is likely to be lost, however, assuming that they are restricted to smaller geographic ranges than plants.

Returning now to the question of the great Linnaean enterprise, do we have the time to finish the classification project of earth's lesser-known taxa (e.g., arthropods, nematodes, mites) before most of them vanish? What would it take to accomplish this task? Recently E. O. Wilson (1988) assumed that there are, at most, about 1,500 systematists competent to deal with tropical taxa. Assuming an average output of new descriptions by this subset of taxonomists of about five per year (this being the historical average, assuming that the effort began a little over 200 years ago), or 7,500 total descriptions per year, and given there are 30 million more tropical species to collect, describe, and classify, it would take 4,000 years to do the job at the current level of effort. (The total number of animal species from all regions described each year is about 10,000.)

Next, let's assume that it is possible to mobilize the necessary economic resources and the educational and scientific talent to increase vastly the number of tropical arthropod taxonomists from 1,500 to a whopping 15,000 "barefoot taxonomists" (Soulé, 1989), thus increasing the output of descriptions of new tropical species from 7,500 to 75,000 per year, or 205 per day. Ignoring the potential information glut and the blizzard of reprint requests, the task would still require 400 years using current procedures. Recall that we have only two or three decades to get the job done, assuming current rates of habitat loss.

So much for this Quixotic brute force option. The training of huge numbers of potentially unemployable systematists is futile, and it cannot begin to meet the extinction challenge. It is also futile to continue the task of describing biological diversity in the manner of the 18th Century, writing, in other words, the slightly premature obituaries of millions of bugs and worms and those of a few thousand randomly selected, undescribed species of plants and vertebrates.

I am not saying that we shouldn't be putting more resources into training taxonomists. Quite to the contrary. For most taxa, there are obviously too few specialists and the need for them is growing rapidly. In addition, our institutions are underfunded; many museums, herbaria, zoos, and botanic gardens have not been able to compete with fashionable "big science" projects, such as mapping the human genome, "star wars" strategic defense technologies, and huge particle accelerators. Finally, we are tantalizingly close to wrapping up several taxa (including plants, vertebrates, some marine phyla, and a few insect groups), and these groups must be completed as soon as possible, so that biogeographic and evolutionary analyses can be based on complete data sets.

Nevertheless, the twin crises of "too many species and too much extinction" will not be solved by the mindless cloning of thousands of taxonomists. Priorities must be established (Raven, 1977; NAS, 1980; Soulé & Kohm, 1989). For systematics and other organismic disciplines, it is not "business as usual" in the closing years of the 20th Century.

Barriers to a Revolution in Systematics

In responding positively to these twin crises, we must look inward as well as outward, confronting

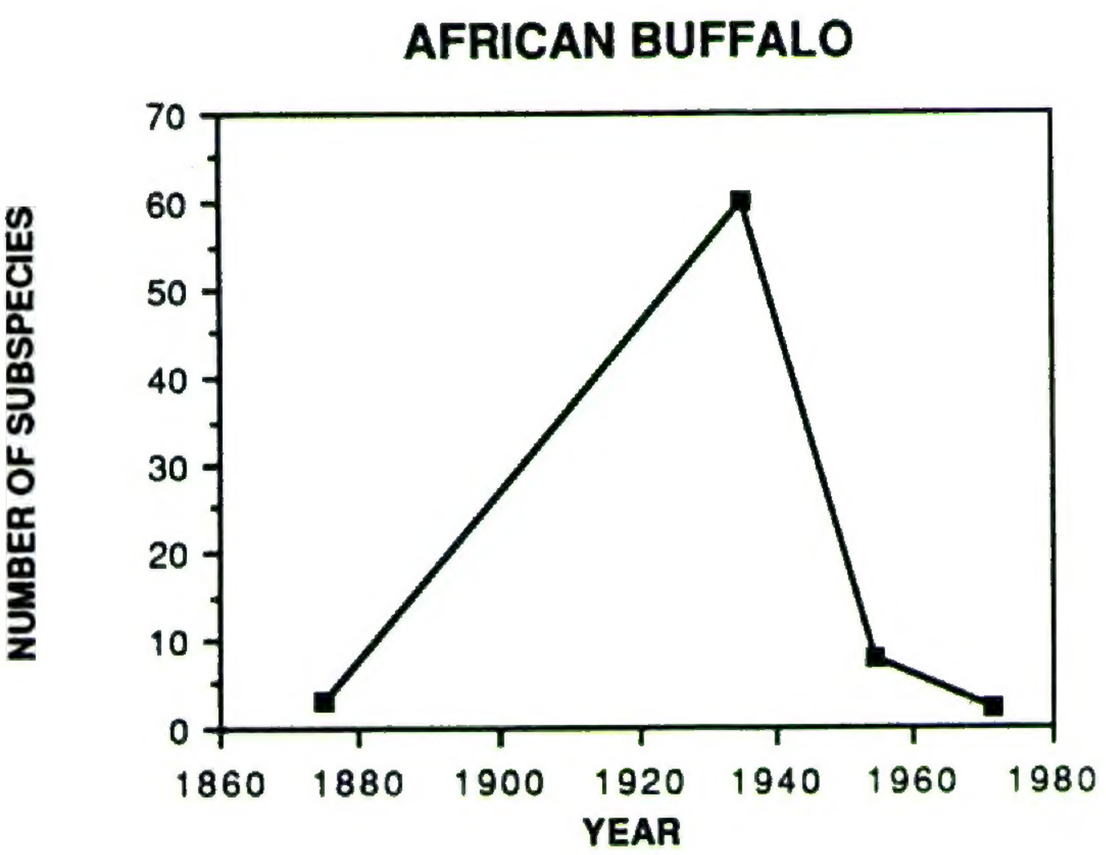

FIGURE 1. An example of excessive splitting for *Bubalus caffer*, the African buffalo. See text.

intrinsic and extrinsic problems. One intrinsic issue is our rhetoric.

EXTINCTION HYPERBOLE?

I am concerned that some of our own rhetoric may come back to haunt us. There is no doubt that humans are initiating a massive spasm of species extinction, and that the rates of extinction may be on the order of 100 species per day in a few decades. But in our panic and despair are we consciously or unconsciously obscuring the complexity of the catastrophe? Is there a conspiracy of silence on the issue of the identity of most of these species?

To biologists, the fact that more than 95% of these threatened species are arthropods and nematodes hardly makes the problem less serious, but to the man on the street, this bit of information would change matters considerably. Such little critters don't arouse a lot of public concern—just the opposite. Most people don't consider arthropods and helminths to be animals. Most people, if they knew this truth about the upcoming extinction spasm, would probably say "good riddance."

Among the more popular taxa, plants and vertebrates, the losses will not be in the millions nor will they come close to approaching a rate of extinction of 100/day. The point that we need to make is that there aren't millions of kinds of birds and mammals. In fact, there are precious few. Relative to the vast number of beetle and mite species, there is hardly a handful of these vertebrate relatives.

On the other hand, we need to explain that: (1) you don't have to have warm blood to be an animal, (2) these"creepy" species have the same right to existence as their green and charismatic cousins, and (3) the demise of vast numbers of bugs and worms is signaling the loss of habitat and ecosystem services (Ehrlich & Ehrlich, 1981) on which all other species, including humans, depend.

ANACHRONISMS AND CHALLENGES

The closet of systematics has more than its share of skeletons. For example, many systematists have pointed out that taxonomy fell into disrepute in the early decades of this century because an extreme form of typology prevailed that led to the application of species and subspecies names to the most trivial intraspecific variants. (The field is still plagued by pockets of extremists.) As shown in Figure 1, for example, some people apparently got a little carried away in describing "new" African buffalo. The zenith of "splitting" was reached in about 1935 when Zukowsky on one occasion gave different, new racial names to the two horns on a single African buffalo *Bubalus caffer* (Ansell, 1971).

We may smile at the excesses of the past, but these excesses are symptomatic of a perennial debate—the species problem. Should every geographic (evolutionary) entity be elevated to species rank, as Cracraft (1983) suggested? Some conservation issues would be instantly solved by such a solution, at least in theory. For example, if subspecies no longer existed, there might be less debate about whether they should be interbred in propagation projects. Of course, it is a delusion to think that this would really solve the problem, because genetic relatedness would still be a matter of degree. Fortunately, many zoos have already adopted genetic rather than strictly taxonomic criteria for such matters (Benirschke et al., 1980; Ryder, 1986; Ryder et al., 1988).

Practices in taxonomy are changing, but are they changing fast enough (Ehrlich, 1964; NAS, 1980)? Methodological stability in such a quasi-legalistic field is commendable, but there must also be sufficient flexibility to accommodate changes in technology and other conditions. For example, the methods for storing museum specimens (most specimens are still preserved as dried organs or as bleached cadavers—in biochemical terms, degraded protein and decomposed DNA) must take into account advances in technology as well as the unfortunate fact that many of today's specimens will become proxies for tomorrow's extinct taxa. Of what value will these specimens be to a 22nd-Century biologist? Put another way, how much more valuable would they be if they were biochemically intact? This is not to say that specimens preserved in the traditional ways (drying, fumigating, denaturing) lack scientific value. DNA fragments can be recovered from specimens that have been in alcohol for decades (Pääbe, 1985), but this

bit of serendipity should not be used as an excuse to decelerate the rate of conversion in many museums to more modern methods of preservation. These days, a collector without dry ice or liquid nitrogen is an anachronism.

"THERE ISN'T TIME FOR MORE RESEARCH"

Extreme anxiety can also be a barrier to change. If the field of systematics is to live up to its potential in the campaign to preserve the diversity of life forms, then it cannot fall victim to slogans born of ignorance. To be specific, one often hears that we already know enough—that we have enough knowledge about the systematics, biogeography, natural history, ecology, and genetics of organisms and ecosystems to establish a rational and comprehensive set of nature preserves that would protect most species from the coming Armageddon. It is asserted that there isn't time to indulge in research—we must simply buy more land and lock it up. Is this true? Do we already know enough to protect biological diversity?

We don't. Research in conservation biology during the last 15 years has altered fundamentally the design criteria and management objectives for protected areas. The rising curve of new, management-relevant discoveries shows no sign of asymptotic approach. Why do I raise this issue here? It is not to point the finger at systematists, who are rarely the perpetrators. Rather it is to enlist the support of systematists for conservation biology *sensu lato*.

Many kinds of knowledge are necessary for the successful design and management of protected areas and propagation projects. The first step in many situations is to describe, inventory, and map biotic diversity. This is because the exact locations of reserves are critical, particularly if the objective is to protect the maximum number of species. The entire conservation enterprise depends on systematists and biogeographers for guidance about where to place reserves, particularly in regions where there exist "hot spots" of endemism and species diversity (Diamond, 1986; Gentry, 1986; Myers, 1988; Soulé & Kohm, 1989).

On the other hand, the *maintenance* of biodiversity in a fragmented landscape is a more complex matter. It depends on scientific progress along many fronts, among which systematics is just one. Even if a reserve is in the right place, it will gradually lose many of its species unless managers are attuned to the effects of climatic change, fire regimes, siltation and sediment load (in marine and aquatic systems), patch dynamics, sea level rise, pollution, edge effects, viability of keystone species, loss of mutualists, migratory life cycles, and current and potential human interactions with species and wildlands. Ignorance of these and other phenomena will produce a bitter harvest of conservation failures and wasted resources. It goes without saying that most of the above kinds of research depend on a taxonomic foundation (Boom, 1988).

Ecological research in the last decade has led to profound changes in the ways that conservation projects are designed and managed. For example, only recently have we realized the ubiquity of the deleterious effects of edges. The effective size of a reserve is often much smaller than its map size would indicate because many diversity diminishing agents penetrate great distances into reserves. Many of these edge effects are only beginning to be understood. For example, Appanah (1987) pointed out that meliponid bees nesting as far as 1 km from the edge of a reserve were returning to their nests with 100% pollen from plantations. Because these bees are important tree pollinators in the forests of south Asia, such behavior could lead to widespread reproductive failure and the gradual die-off of forest interior species.

The future status of the Everglades National Park at the southernmost tip of Florida, one of the richest landscapes in North America, offers an example of how recent discoveries can and should modify our management methods and priorities. Larry Harris (pers. comm.) has pointed out that the gradient in this part of Florida is 1:25,000, and that, given the accelerating rates of sea level rise (Titus, 1986), there is virtually nothing we can do to prevent the disappearance of most of this park under Florida Bay and the Gulf of Mexico in 50 to 100 years. There are many endangered species in the Everglades, but existing recovery plans have ignored this inevitable source of habitat loss and its implications for population viability.

Genetics provides many examples of how very recent studies have altered the management of conservation projects. Genetics was virtually ignored by managers until the late 1970s. A few prophets (e.g., Frankel, 1974; Seal, 1978) had earlier warned of the hazards of inbreeding and the loss of genetic variability, but there were hardly any data from rare or captive species, and there were certainly no concrete guidelines of use to managers. Only in the last 10 years has evidence of widespread inbreeding depression in captive groups been uncovered (Ralls et al., 1988, and references therein). It is only in this decade that guidelines and protocols for wild and captive stocks have been suggested (Franklin, 1980; Soulé, 1980;

Frankel & Soulé, 1981; Schonewald-Cox et al., 1983; Templeton & Reed, 1984; Lande & Barrowclough, 1987). Notwithstanding that the original caveats accompanying these principles and guidelines have been largely ignored, it is impressive how rapidly genetics has been assimilated into the mainstream of captive breeding, recovery planning for endangered species, and the management of small groups of large animals.

The problem is that once assimilated, people tend to take such information for granted, and to forget how important conservation biology has been in shaping current management practices. During crises, the value of past research is often ignored. In doing this, we commit an even graver and more perilous sin: discounting the value of future research.

Those who believe that we cannot simultaneously secure land *and* do more research fail to appreciate that, metaphorically, the storage of a precious book or painting in a secure vault does nothing to prevent its gradual, chemical deterioration. To put aside land without knowing how to manage it is folly. It should be noted parenthetically that agencies like the National Science Foundation (NSF) may be legally barred from purchasing lands in developing countries, but they are not barred from funding research that would help insure the protection of biotic diversity on such lands.

In our panic to secure the few remaining bits of wild nature, we should not forget that our understanding of biological diversity, particularly in the tropics, is shockingly superficial. Therefore, we have no choice but to proceed urgently to study the basic mechanisms that fuel, threaten, and maintain the biotic complexity of this planet. Given the rate of habitat destruction, much of this research must be accomplished within the next few years or decades at most. The maintenance of biotic diversity, in situ and ex situ, will depend largely on the quality and quantity of these studies.

The next step is to ascertain the most critical research needs. Recently, a workshop sponsored by NSF was convened by the Society for Conservation Biology (SCB) at Hawk's Cay in Florida to frame a report on research priorities in conservation biology (Soulé & Kohm, 1989). Following are the most pressing and important initiatives and research needs agreed upon at the workshop. Systematics is at the heart of the first priority.

1. *A crash program to carry out extensive surveys and mapping to identify areas that are critical for the protection of nature and genetic resources.* Reiterating the recommendations of an earlier report (NAS, 1980), these critical areas should be defined in terms, among others, of their high biotic diversity, high levels of endemism, or imminent destruction of critical or unusual habitats and/or biotas. These studies should emphasize taxonomic groups that are better known or those that would indicate parallel biogeographic patterns in groups less amenable to censusing. A byproduct of this research could be critical information on the rates of deforestation and other forms of habitat destruction.

2. *It is particularly important to understand how natural systems "work," especially in the tropics.* Therefore, the group called for the immediate establishment of a small number (perhaps four to eight) of research sites in the tropics in order to carry out a coordinated program of comparative research on populations, communities, and ecosystems in relatively pristine and secure situations. The workshop participants agreed with the authors of the authoritative NAS report, *Research Priorities in Tropical Biology* (1980), in recommending the establishment of several major ecological research sites in the humid tropics where in-depth, long-term, and globally coordinated studies are supported.

These focal sites would be especially valuable as sources of long-term, baseline information on global and ecological processes. The SCB/NSF workshop also recommended the active participation of local students, professionals, and institutions in this program and other research projects in their developing countries. One reason that the group did not recommend a large number of such sites is because there are too few researchers with the necessary expertise.

3. *Studies at all spatial scales to assess the kinds, mechanisms, magnitudes, and impacts of humans on ecological systems.* Here are included the effects of habitat fragmentation, biotic mixing (introductions), and air, water, and marine pollution. These studies should focus on the development and evaluation of alternative means of exploitation and land/water use, with the goal of improving human welfare while minimizing environmental deterioration and the destruction of biological diversity.

4. *Studies on the physiology, reproduction, behavior, ecological interactions (including diseases), and viability of individuals, populations, and species have been essential in the protection and management of reserves and other wildlands.* The group urged the enhanced support

for research that focuses on these fundamental, species-level processes and relations, especially with regard to species of critical ecological or economic importance.

5. *Education in conservation biology, wildlands management, and related areas with the objectives of training basic scientists and natural resource managers, particularly in tropical, developing countries.* Much of this training should occur locally and regionally, and should benefit local institutions and strengthen the conservation and management infrastructures in developing nations.

The above list omits direct mention of global phenomena that affect landscape arrangement and habitat quality. These phenomena are of paramount importance for the protection of biodiversity, and are being intensely studied by other groups of experts.

To summarize, the maintenance of biotic diversity in protected areas and in ex situ facilities will depend on many disciplines. Success will require a level of tolerance and a degree of scientific pluralism that are uncharacteristic of organismic and environmental biologists. Systematists should take the lead in this "new age of biological brotherhood."

What Roles for Systematists in the Biodiversity Crisis?

Granting the central role of systematics in conservation biology, what can be done to involve more systematists (and other organismic biologists and ecologists) in the campaign for the protection of biological diversity? First, let me restate the problem: there are far too many taxa to be named and classified in the short time remaining (Ehrlich, 1964). Systematists might consider the following suggestions, none of which are original with me.

1. *For relatively unknown groups like tropical insects, concentrate on a few "representative" taxa*, hoping that the phyletic, morphological, biogeographic, and ecological patterns manifested by these taxa are typical of related ones. Which groups should be chosen? Who would choose them? How should interim conclusions be validated? Answers to these questions require an unprecedented level of cooperation, compromise, and organization.

2. *Focus on ecologically keystone and indicator taxa and their mutualists.* In other words, adopt an ecological approach, letting nature's structure help shape taxonomic priorities, in contrast to the present haphazard selection process driven by economics (agriculture and entomology), personal whims ("I *like* sceloporine lizards"), and theoretical issues in evolutionary biology.

One such approach is to concentrate on taxa containing keystone species. Within the last decade or so, conservation biologists have emphasized the critical ecological roles of keystone species. Defined operationally, a keystone species is one that, by its effective absence from a system, results in the virtual disappearance, directly or indirectly, of several other species, causing, in other words, an extinction cascade. "Several" is undefined, and further work on the utility of this concept is obviously necessary.

In addition, the concept is in need of a great deal more empirical and theoretical analysis. Several avenues are being pursued (Mills & Soulé, in prep.). For example, one can divide keystone species into two categories, *trophic keystones* and *structural keystones*. The absence of the former kind will lead to dramatic changes at one, two, or more trophic levels below. The absence of structural keystones leads to changes in habitat, which in turn causes significant shifts in abundance of other species that may or may not be trophically connected to the keystone. Table 1 lists some of the categories of keystone species and gives examples of the likely consequences of their effective loss (including human-induced rarity) from a community.

Effective management of protected areas depends on an understanding of the interactions of keystone species. Terborgh (1986) found, for example, that figs and palm nuts are keystones in a Peruvian tropical forest, where they may be the only food resources during the annual period of food scarcity. Palm nuts escape from all but a small group of specialist species that are either large and with powerful jaws or else can gnaw the nuts. Thus, among the few customers are peccaries and capuchins, comprising ca. 30% of the total biomass of fruit-eating animals. Fig trees, though they fruit irregularly, are often keystone producers; figs are heavily consumed by all larger primates, procyonids, marsupials, and many birds. Terborgh (1986) concluded that a group of only 12 plant species (out of 2,000) maintains almost all large frugivores for about three months of the year.

If we are to succeed in the protection and management of the remnants of biodiversity, there is an urgent need to refine and deepen our understanding of keystone species, especially in the tropics where most of the planet's biological riches exist

TABLE 1. Some kinds of keystone species and the effects of their effective removal from a system.

Keystone category	Effect of removal	Examples
Trophic/resource keystones		
Top predators	Large increases in the abundances of prey species and smaller predators, and subsequent extirpations of some of the latter's prey species	Felids, canids, fishes
Pollinators and other mutualists	Failure of reproduction and recruitment in certain plants; disease and dieback of plants, bleaching in reef-building corals, etc.	Hymenoptera, Lepidoptera, symbiotic algae, fungi
Providers of essential resources	Local extirpation of dependent animals, including fruit- and nectar-eating species during times of scarcity	Trees, such as *Ficus* and trees that provide nesting and hibernating sites
Structural keystones		
Species that maintain landscape features	Disappearance of water holes and wallows, ponds, etc.	Tapirs, beavers, alligators
Herbivores that prevent succession	Return of cover and decrease in habitat diversity; disappearance of species dependent on early successional habitats and resources	Moose, elephants, rabbits

and are currently at great risk. Current research efforts in this regard are pitifully inadequate, and the low level of funding for basic research in tropical ecology in general is simply scandalous.

3. *Focus systematic work on phylogenetic relicts or other evolutionary outliers.* Evolutionary outliers contain precious information in their genotypes and phenotypes and should rank at the top for systematic attention. Obvious target taxa include oligotypic marine phyla, proboscidians and other remnants of the great mammal radiation, and the last representatives of genera and families that are about to disappear, such as *Hibiscadelphus* in the Hawaiian Islands (Gentry, 1986, and references therein).

4. *Focus systematic work on local endemic taxa inhabiting vulnerable environments.* Habitat fragmentation and regional and global climate changes will eliminate local endemics, including those that inhabit estuaries, reefs, boreal mountain tops in low latitudes, and tropical forests. Other kinds of biogeographic cul-de-sacs harbor some interesting examples. A case in point is the fauna that is restricted to the relatively cool waters of the north end of the Gulf of California, Mexico (Brownell, 1986; Perrin, 1988). As global warming develops, many of these taxa, including the porpoise *Phocoena sinus*, are likely to be squeezed out of existence, trapped between the land on the west, north, and east, and the warm waters to the south.

5. *Develop new (interim) approaches for describing and classifying*, especially for groups like tropical arthropods for which traditional approaches are too slow by orders of magnitude and for which binomials can wait (Soulé, 1989). I'm not speaking of DNA fingerprinting using restriction fragment length polymorphisms, nor the use of mitochondrial DNA, nor the use of electrophoresis for the detection of protein variants and the measurement of their frequencies, nor DNA hybridization studies, nor similar techniques. These are all too costly and time-consuming. I am referring to automated methods for screening, cheaply and efficiently, very large numbers of specimens and assigning them to taxa of convenience. These methods might include three-dimensional tomography for computerized clustering based on morphology and automated chromatographic screening for clustering based on biochemical patterns in such tissues as cambium and hemolymph.

Other suggestions have been made that would enhance data retrieval, comparability, and depth. For example, data entry formats should be developed by international teams of systematists and conservation biologists (ecologists, geneticists, and biogeographers) to ensure that the data will be useful to those asking different sorts of questions. Unless such a team approach is implemented, and such formats and methods are standardized by international agreement, much of the current investment in data banks for systematics will be wasted.

Education is also a high priority. Systematists are in a better position than most biologists to plant the seeds of a conservation ethic. They are often in a position to train local people and to engage leaders in discussions about the latter's biotic patri-

mony. As teachers, systematists can profess the love of nature to students, the younger the better.

On Our Real Work

The last of the preceding proposals brings me to my final point—it is OK for systematists to speak of love and beauty. It is even OK for systematists to express emotions in public. Real adults are not afraid of labels like "emotional" and "sentimental." Real adults have left behind the Rambo developmental stage and its preoccupation with *machismo*. I don't mean to deny or even to denigrate the harder aspects of human nature. The "right stuff" is adaptive in many circumstances, and ambition can be harnessed just as well for the protection of creatures as for their destruction. Nevertheless, I believe that maturity includes the courage to embrace publicly stewardship as a "familial" responsibility. Giving succor to the earth is our final and most adult task, our real work (Snyder, 1980).

Some may wonder how can we be effective, let alone charismatic, in communicating these feelings of kinship and concern in our work (Wilson, 1984; Soulé, 1988)—our research and teaching—without appearing foolish. Perhaps, we can't. Perhaps, for a real adult, appearing foolish to less mature peers is as inevitable as work itself.

By "work" I am referring to our careers as well as to our real work, which is to love the earth by preserving its actual and potential diversity. Regarding career, Freud said some interesting things about work and its relationship to happiness. For him *Liebe und Arbeiten*, love and work, were not separate compartments. Freud considered the professional work of "civilized" men and women, with all its grasping for recognition and respect, as sublimation for the giving and receiving of love. If there is some truth in this, if each of us wishes to contribute something of lasting value to the world (giving love), and to be acknowledged for it (receiving love), then we biologists are fortunate indeed. It is relatively easy for us to express our love of biotic diversity through our research, writing, mentoring, and teaching. And in return, there is not only peace of mind, but also the gentle fellowship of coconspirators. For us, conservation biology *is* the synthesis of love and work.

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THE GENETIC CONSEQUENCES OF HABITAT FRAGMENTATION[1]

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ABSTRACT

The natural habitats of many species have become fragmented into small "islands," principally by human activities. In this paper we discuss the long-term genetic and evolutionary consequences of fragmentation as inferred from studies on populations that have undergone natural habitat fragmentation in the Ozark Mountains. The Ozarks are the highest land formation found in the midwestern United States. Because of the absence of major geographical barriers around the Ozarks, plants and animals from diverse parts of the continent have been able to invade the area during post-Pleistocene climatic periods. Many of these invasions were short-lived, but the geological and topographical complexity of the Ozarks provided numerous relictual habitats. As a consequence, natural habitat fragmentation occurred for many species, and the fragmentation has often persisted for thousands of years. The genetic and ecological consequences of habitat fragmentation depend critically upon whether or not habitat fragmentation results in a complete cessation of dispersal between the habitat islands. If habitat fragmentation results in the complete genetic isolation of habitat islands, then each "island" becomes demographically independent and local extinction can occur. When there is no opportunity for recolonization, an "extinction ratchet" is possible in which each local extinction brings the global population irreversibly one step closer to total extinction. It is therefore critical to know if habitat fragmentation actually prevents dispersal or not. Unfortunately, studying dispersal patterns directly is usually not feasible. We show how genetic surveys can be used to answer this question. Given demographic fragmentation, we also show how genetic surveys can pinpoint species at high risk for local extinction. These suffer the most severe genetic consequences from habitat fragmentation, such as a drastic loss of genetic variability within habitat islands and inbreeding depression. On the positive side, the genetic variation of a fragmented species is not totally lost but is often present as fixed differences between different local populations. Indeed, a fragmented population is subject to less global loss of genetic variation than an equally sized panmictic population. Consequently, as long as the rate of local extinction is relatively small or counteracted by a recolonization program, a fragmented species can preserve almost all of its genetic variation at the global level for long periods of time. We discuss the optimal design for a recolonization program to prevent global extinction and to maintain high levels of global genetic variation.

As human use of the environment expands, the amount of habitat available for natural communities decreases and the remaining habitat becomes increasingly fragmented. That is, habitats become subdivided into "habitat islands" surrounded by different, usually human-altered, environments. Many tropical and temperate habitats have already been extensively fragmented, and the amount of fragmentation will increase substantially in the foreseeable future.

Conservation biologists are concerned about habitat fragmentation because of its potential to increase extinction rates as predicted by island biogeographic theory (MacArthur & Wilson, 1967), because of "Allee" and "edge" effects, and because of its potential to erode genetic variation through genetic drift in small populations and to promote inbreeding depression. Accordingly, there have been several studies on the impact of habitat fragmentation, but most of these have focused on recent, human-induced habitat fragmentations (e.g., Soulé et al., 1988). Because conservation biology is concerned with the long-term maintenance of biodiversity, we must deal with the long-term ecological and genetic consequences of habitat fragmentation as well as the short-term ones. Once we have a clearer idea of what these long-term consequences are, we can address the question of how best to manage species and communities in fragmented habitats in order to preserve biodiversity for thousands of years.

This paper will focus on the long-term (thousands of years) consequences of habitat fragmentation. In order to study this problem, we cannot use

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recent, human-induced, fragmented habitats. Instead we must look for natural cases of habitat fragmentation that have occurred over the last several thousands of years.

The Ozarks as a Natural Laboratory of Habitat Fragmentation

The Ozarks are the highest elevated land mass between the Appalachian and Rocky mountains in North America. The Ozarks are located primarily in southern Missouri and northern Arkansas, and extend into southern Illinois and eastern Oklahoma. Four features make the Ozarks an ideal natural laboratory for study of the long-term consequences of habitat fragmentation.

The first feature, geological complexity, provides a mosaic of substrates for natural communities. About 1.5 billion years ago, several volcanoes were formed above a hot-spot in what are now known as the St. Francois Mountains in southeastern Missouri (Kisvarsanyi, 1980). Subsequently, this area was periodically invaded by shallow seas, which were associated with the deposition of various sedimentary strata, such as limestone and sandstone. As a consequence, the Ozark area has a complex mixture of igneous and sedimentary rocks, all of which are currently exposed at certain locations.

The second feature is topographical complexity. After the creation of an extensive plateau by sedimentary deposits, the Ozark region has been subjected to erosion by surface and underground streams. The surface topography of the Ozarks was thus transformed from a plateau into a series of ridges and valleys through which flow numerous streams, and which are interspersed by karst features, such as sinkholes and collapsed cave systems. This topographical complexity coupled with the geological complexity mentioned above create much potential habitat diversity in terms of soil types, drainages, and microclimates.

The third feature is the extensive climatic changes that have occurred in this region during and after the Pleistocene Epoch. From about 18,000 to 12,000 B.P. (before present), a boreal spruce forest existed in this area, only to be replaced by a predominantly oak-hickory forest. However, during the Ipsothermal Maximum of 8,000 to 4,000 B.P., the area was hotter and drier than at present, and the oak-hickory forest retreated and was replaced by prairies and deserts. At the end of the Ipsothermal Maximum, the oak-hickory forest reinvaded as the climate became cooler and wetter (COHMAP Members, 1988).

During these climatic fluctuations, plant and animal communities were free to move in and out of the Ozarks because of its fourth critical feature: the absence of major barriers to dispersal around the Ozarks. Many diverse organisms were able to enter the Ozarks during climatically favorable periods, only to be isolated from their main distribution ranges when the climate changed again. Because of the great potential for habitat diversity, relictual populations of many of these species were able to survive in the Ozarks. These relictual populations are found in naturally fragmented habitats that have been cut off from the remainder of their species distribution for a few to several thousands of years. We have been examining several species with relictual Ozark distributions for our studies on habitat fragmentation.

Materials and Methods

Protein electrophoresis was carried out using horizontal starch gel electrophoresis and the methods outlined in Selander et al. (1971) and Thompson & Sites (1986). Gels were prepared by mixing equal volumes of Connaught hydrolyzed starch and Electrostarch, and diluting with gel buffer to a final concentration of 12%.

DNA was isolated as described in Hillis & Davis (1986). This procedure isolates total cellular DNA and thus contains mtDNA and nuclear rDNA. The cellular DNA extracts were digested with various restriction endonucleases using the reaction conditions recommended by the supplier. Agarose gel electrophoresis, Southern blotting, and subsequent hybridizations were carried out as described by Hillis & Davis (1986).

Cryptobranchus alleganiensis. Hellbenders were collected by lifting large rocks and grabbing by hand. Animals were anaesthetized in an aqueous solution of ethyl m-aminobenzoate methanesulfonate, and blood was collected from an incision in the tip of the tail. Blood samples were diluted in a buffer (0.1 M NaCl, 0.05 M tris, 0.001 M ETDA, pH 7.5) and immediately frozen in liquid nitrogen. All hellbenders were released after regaining consciousness except for one or two voucher specimens per river. Blood samples were stored at −80°C until DNA was extracted. Different fractions of the extracted DNA were digested with the following enzymes: BamHI, BclI, BglII, BstEII, DraI, EcoRI, EcoRV, NcoI, PstI, PvuII, SacI, StuI, XbaI, and XmnI. The mtDNA was probed with two homologous clones that contain all but 3.6 kb of the hellbender mitochondrial genome as well as a clone of the entire mtDNA of the frog *Xenopus laevis* (pX131, kindly donated by Dr. Igor Dawid).

Crotaphytus collaris. Collared lizards were collected by hand or by noosing. At the beginning of our work with this species, it was necessary to sacrifice the animals to obtain genetic data. To perform the isozyme survey, 24 animals were collected from across Missouri. Heart, liver, blood, and kidney tissues were used for the isozyme analysis, and skeletal muscle was used for DNA isolation. After this initial survey, all subsequent genetic data were collected from blood samples obtained nondestructively. Blood was collected by piercing the suborbital sinus with a heparinized capillary tube. The blood used for protein electrophoresis was kept on ice until returned to the laboratory. There, the blood was centrifuged for one minute in a hematocrit centrifuge to separate the serum from the red blood cells. The serum was added to an equal volume of distilled water and then frozen for later electrophoresis. The serum was used to score for three different nonspecific esterase loci, two leucine aminopeptidase loci (E.C. 3.4.11.1), two superoxide dismutase loci (E.C. 1.15.1.1), and three general protein loci. The red blood cells were lysed in 1.5 volumes of distilled water and then frozen for later electrophoresis. The red cell gels were scored for an additional esterase locus, alpha and beta hemoglobin, two lactate dehydrogenase loci (E.C. 1.1.1.27), and malate dehydrogenase (E.C. 1.1.1.37).

Blood used for DNA extraction was diluted in buffer and kept either on ice or frozen in liquid nitrogen until returned to the laboratory, where it was stored at −80°C. The extracted DNA used for the rDNA and mtDNA studies was digested with ApaI, BamHI, BclI, BglI, BglII, BstEII, DraI, EcoRI, EcoRV, HincII, HindIII, KpnI, PstI, PvuII, SacI, SacII, StuI, XbaI, and XmnI. The mtDNA was probed with nick translated *Crotaphytus collaris* mtDNA prepared from intact circular mitochondrial DNA isolated from the 24 sacrificed animals by the methods of Lansman et al. (1981). The rDNA was probed with two clones that contained the mouse 18S gene (pFM84) and the mouse 28S gene (PI19), both kindly provided by Dr. Norman Arnheim. Cellular DNA for the analysis of hypervariable VNTR (variable number of tandem repeat) loci ("DNA fingerprinting") was digested with HaeIII and probed with a subclone of the human clone 33.15, kindly donated by Dr. A. Jeffreys.

Trimerotropis saxatalis. Lichen grasshoppers were caught with nets and placed in a cool container until returned to the laboratory, where they were stored at −80°C until being processed for electrophoresis and DNA analysis. Processing involved removing the digestive tract and grinding the internal tissue of the thorax in buffer or distilled water (for the protein electrophoresis work). The only results reported in this paper deal with the enzyme leucine aminopeptidase (LAP) and mtDNA digested with EcoRI.

Results and Discussion

CRYPTOBRANCHUS ALLEGANIENSIS

The numerous spring-fed streams that drain the Ozarks provide a habitat for the largest North American salamander, *Cryptobranchus alleganiensis*, commonly known as the hellbender. With the exception of the Ozark populations, hellbenders are found only in the rivers that drain the Appalachians. Consequently, the Ozark hellbenders represent relictual invaders from the eastern United States. Within the Ozarks, hellbenders are distributed into two disjunct populations. One population inhabits the rivers that drain to the north from the Ozarks and empty into the Missouri River or into the Mississippi River close to its confluence with the Missouri River. Members of this population are classified into the subspecies *C. a. alleganiensis*, the same subspecies found in the eastern United States. The other Ozark population inhabits the rivers that drain to the south from the Ozarks and eventually empty into the Mississippi River to the south of the state of Missouri. These southern Ozark animals belong to their own subspecies, *C. a. bishopi*.

The hellbender is totally aquatic and is incapable of terrestrial dispersal. As a result, not only are the two Ozark populations disjunct from one another and their eastern ancestors, but the two Ozark populations are further fragmented into different river systems within these two drainages. Even within a river, their distibution is very patchy. Adult hellbenders are usually found only in those portions of the rivers that have large, loose rocks on the bottom. Unfortunately, virtually nothing is known about the distribution and dispersal behavior of the larvae, although the adults are quite sedentary (Nickerson & Mays, 1973).

In order to infer the pattern of gene flow in this species, we overlaid genetic surveys onto the geographical distribution of the species. Previous studies (Merkle et al., 1977) using isozyme markers revealed that all hellbenders with a few minor exceptions were monomorphic for the same alleles regardless of capture site. Hence there is simply insufficient genetic resolution with isozymes to address the issue of gene flow. We therefore used

TABLE 1. Variable mitochondrial DNA haplotypes found in various populations of *Cryptobranchus alleganiensis* from Missouri and Tennessee. The first eleven variable sites have been mapped on the mitochondrial genome; a "1" refers to the presence of that site and a "0" its absence. The last three restriction fragment length polymorphisms have not yet been mapped, so small letters refer to distinguishable fragment length patterns.

Restriction sites	Haplotypes							
	A	B	C	D	E	F	G	H
BamH1-b	1	0	0	0	0	0	0	0
BglII-d	1	1	0	1	1	1	1	1
BstEII-b	1	1	0	0	0	0	0	0
EcoRV-b	1	1	1	1	1	0	1	1
-c	1	1	0	0	0	0	0	0
-d	1	1	0	0	0	0	0	0
Stu1-5	1	1	0	0	0	0	0	0
-c	1	1	1	1	1	1	1	0
Xmn1-c	1	1	1	1	0	0	0	0
-d	0	0	1	0	0	0	0	0
-e	0	0	0	0	0	0	1	0
BclI Pattern	a	a	b	b	c	c	c	c
NcoI Pattern	a	a	b	c	a	a	a	a
XbaI Pattern	a	a	b	b	b	b	b	b

restriction site mapping of mitochondrial DNA (mtDNA) because, at least in mammals, it evolves about 10 times faster than nuclear DNA and accordingly has much higher levels of polymorphism (Brown et al., 1982). As shown in Table 1, eight distinct mitochondrial haplotypes were found in hellbenders collected in Missouri and in Tennessee.

Table 2 shows the geographical distribution of these variants within hellbenders, and Figure 1 portrays these data graphically. Figure 1 also gives a maxium parsimony unrooted cladogram of the eight haplotypes (with a consistency index of 1) as determined by hand. As evident in Figure 1, there is no overlap in the haplotypes found in Tennessee with those found in Missouri. We therefore conclude that the Missouri population is isolated completely from the eastern portion of the range of the species. Moreover, there are no shared haplotypes between the northern and southern drainages of the Ozarks, and as the cladogram shows, the northern and southern haplotypes correspond to distinct branches that are well separated from each other by seven substitutional events. This implies that there is no gene flow between the northern and southern drainages within the Ozarks. Figure 1 also implies that there is restricted gene flow between some of the rivers within the southern and northern drainages. The two southern rivers are fixed for two different haplotypes that define a single branch in the cladogram but that are separated from each other by four substitutional events. This pattern indicates that there is no gene flow between these rivers. In the north, the Niangua River populations are fixed for the B haplotype that is found in only low frequencies in the other northern rivers. However, there are no statistically significant differences in haplotype frequencies among any of the other northern sites, so the possibility of some gene exchange among the Gascanade, Big Piney, and Meramec rivers cannot be excluded. Data from three rivers with multiple collecting sites show no significant differences among sites within a river. This suggests that the patchy distribution of adults within a river does not cause genetic isolation.

In summary, the pattern shown in Figure 1 implies that Missouri populations are genetically isolated from the eastern species range and that northern and southern Ozark drainages are isolated from one another. In addition, many rivers define genetically isolated populations from nearby rivers, but local populations within a river are not genetically isolated from one another.

Hence, by overlaying the genetic survey results upon the geographical distribution of the populations, we have been able to infer much about when habitat fragmentation results in genetic isolation and when it does not for this species. This conclusion would be virtually impossible to make from traditional dispersal studies because of the extreme difficulty of following the fate of larvae in this species and because the adults are extremely long-lived, which invalidates the use of short-term studies. These problems are not limited to hellbenders and occur frequently with other species. For example, one of the better dispersal studies ever done with amphibians involved marking over 25,000 tadpoles and metamorphosing Fowler's toads, which after five years of work resulted in the recapture of 37 adults (Breden, 1987). However, given sufficient genetic resolution, the same types of inferences about genetic subdivision can be made from a genetic survey of a much smaller number of adults.

We believe that using genetic surveys to infer when habitat fragmentation results in complete genetic isolation and when it does not represents one of the most important applications of genetics to the problem of habitat fragmentation. The reason for this importance lies in the fact that the long-term ecological and genetic fate of a fragmented population depends critically upon whether or not there is genetic isolation between the habitat islands, as will be illustrated by our next example.

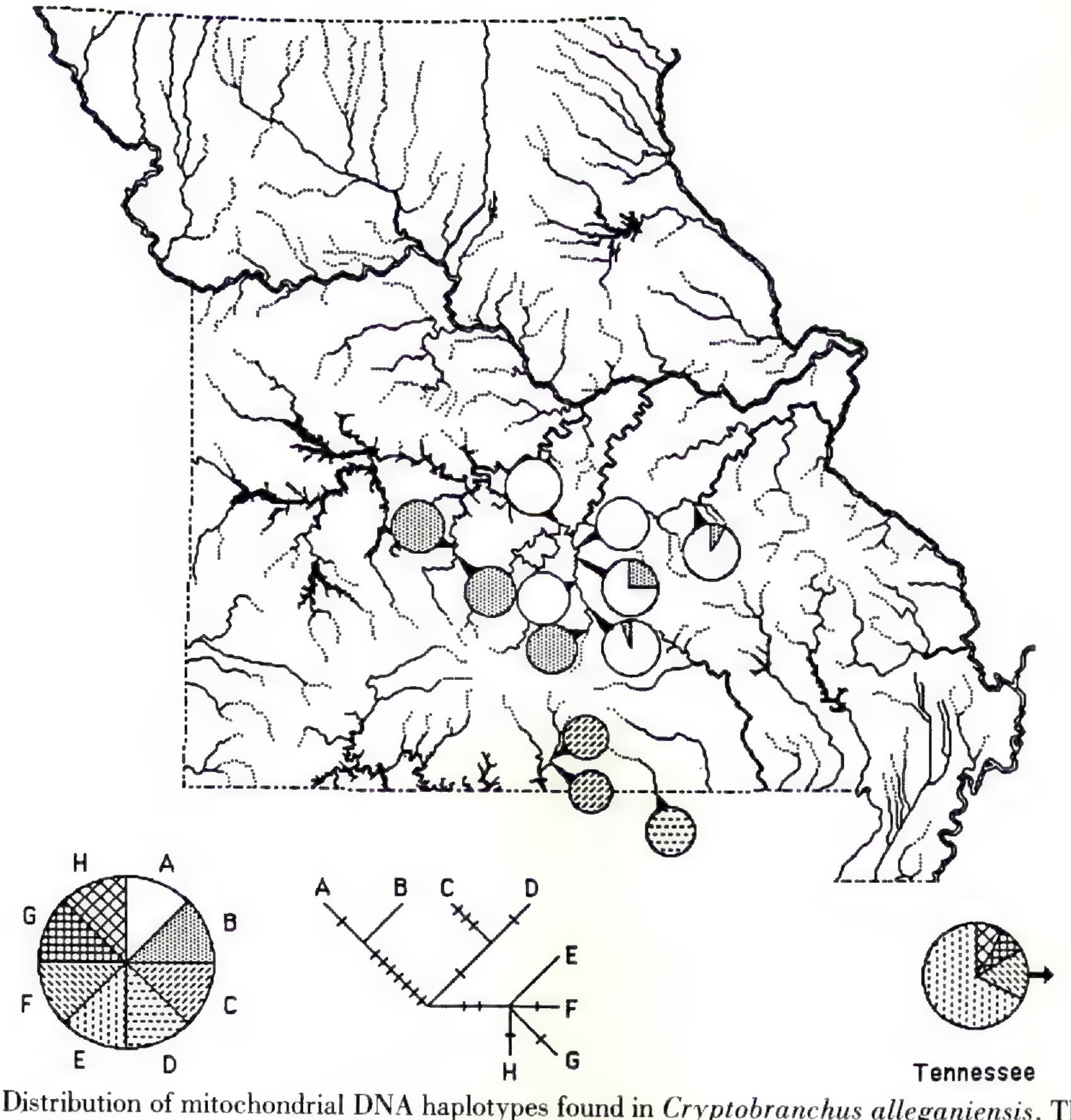

FIGURE 1. Distribution of mitochondrial DNA haplotypes found in *Cryptobranchus alleganiensis*. The map shows the major river systems in Missouri. The pie diagrams indicate the mtDNA haplotype frequencies at various collecting sites from the data given in Table 2. The maximum parsimony cladogram (with a consistency index of 1) that connects the various haplotypes is shown at the bottom.

CROTAPHYTUS COLLARIS

The main range of collared lizards is in the southwestern United States and in northern Mexico. They also reside in highly fragmented populations scattered thoughout the Ozarks. These desert animals most likely invaded Missouri during the Ipsothermal Maximum of 8,000 to 4,000 years B.P. With the reinvasion of the oak-hickory forest around 4,000 B.P., these lizards were only able to survive in Missouri in relictual, desertlike habitats known as glades. Glades form on exposed outcrops of sedimentary or igneous rock, usually near tops of ridges with southerly or southwesterly exposures. The poor, rocky soil of glades inhibits tree growth, and the rocky, southerly exposures create a very dry, hot microhabitat. As a consequence, a large number of animals and plants normally found in deserts or dry prairies are also found in Ozark glades, including collared lizards.

Glades vary in size from less than an acre up to several hundreds of acres (Nelson & Ladd, 1981). The larger glades tend to be on dolomite and have a more prairielike flora and fauna than the more desertlike igneous glades. Collared lizards are one of the few glade endemics that can inhabit both of these major glade types. The dolomitic glades are also more susceptible to forest invasion, and with the advent of forest fire control in historic times, there has been a secondary phase of fragmentation of the dolomitic glades due to forest encroachment (Beilmann & Brenner, 1951). Consequently, with the collared lizards, a primary phase of habitat fragmentation occurred 4,000 years ago followed by a secondary phase on dolomitic glades within the last two centuries.

As with the hellbenders, we can use genetic surveys to infer when habitat fragmentation results in genetic isolation. Table 3 summarizes the results of genetic surveys using protein electrophoresis on 17 loci and restriction mapping of nuclear ribosomal DNA (rDNA) and mtDNA using 19 restriction enzymes. The amounts of genetic variation found with any one of these techniques are modest, with the discovery of only one polymorphic protein locus and four haplotypes each for the rDNA and

TABLE 2. Geographical distribution of mitochondrial DNA haplotypes found in various populations of *Cryptobranchus alleganiensis* from Missouri and Tennessee. The haplotype designations are given in Table 1.

Locations	Numbers of animals with haplotypes: A	B	C	D	E	F	G	H
Northern Missouri								
Big Piney River								
Barton Branch	0	1	0	0	0	0	0	0
Boiling Spring	23	1	0	0	0	0	0	0
Slabtown Spring	11	0	0	0	0	0	0	0
Spring Creek	9	3	0	0	0	0	0	0
Devils Elbow	11	0	0	0	0	0	0	0
Gasconade River	12	0	0	0	0	0	0	0
Niangua River								
Site 1	0	14	0	0	0	0	0	0
Site 2	0	3	0	0	0	0	0	0
Meramec River	21	2	0	0	0	0	0	0
Southern Missouri								
North Fork of White River								
Site 1	0	0	14	0	0	0	0	0
Site 2	0	0	3	0	0	0	0	0
Spring River	0	0	0	6	0	0	0	0
Tennessee								
Little River	0	0	0	0	9	2	1	0
Beaverdam Creek	0	0	0	0	7	0	0	1

mtDNA (Table 3). Although no one genetic system detects much variation, the pooled systems provide a reasonable degree of genetic resolution, as shown in Figure 2. The joint pattern strongly suggests that different glades are genetically isolated from one another. As Figure 2 shows, almost all of the genetic variation is found as between-glade differences.

Strong genetic differences can exist on even a very local scale. For example, the lizards on Mina Sauk glade are fixed for rDNA and mtDNA haplotypes different from those for which the lizards on Proffit Mountain are fixed, despite the fact that these two areas are only about eight miles apart as one would walk along ridge tops (the most probable dispersal route for lizards). Even on Proffit Mountain, there seems to be strong genetic differentiation between glades only a quarter of a mile from one another, although small sample sizes make this a tentative conclusion.

There thus seems to be extreme genetic fragmentation in the northern Ozarks. There is likewise evidence for extreme genetic fragmentation in southwestern Missouri. The populations on Dewey Bald, Hercules Glade, and Glade Top Trail are all fixed or nearly fixed for different genotypes. The only significant geographical pattern is that the three glade populations on Glade Top Trail all share a unique genotype. Since these three dolomitic glades were undoubtedly a single glade before forest fire control this genetic sharing is not surprising. Moreover, the Lookout population on Glade Top Trail is the only polymorphic population for these genetic systems found on a natural glade (as will be discussed shortly, the Proffit Mountain population is not inhabiting a natural glade). This observation supports the hypothesis that the Glade Top Trail populations were a single, large population until very recently.

As Figure 2 summarizes, the glades isolated at the end of the Ipsothermal Maximum display a genetic pattern that suggests complete genetic isolation. The lack of any clear geographical pattern to how this between-glade variation is distributed indicates that the isolation at the end of the Ipsothermal Maximum was very rapid; that is, all the glades became isolated from one another more or less at the same time, so that there is no evidence for the pattern expected under an isolation by distance model.

Once again, we have an example of how genetic surveys can be used to determine the extent to which habitat fragmentation causes genetic fragmentation. In the case of the collared lizards, this genetic fragmentation appears to be more severe than it is for the hellbenders. The primary ecological consequence of complete genetic isolation is demographic fragmentation. By this, we mean that the dynamics of population growth, age structure, etc., within a habitat island exerts no direct influence upon the comparable demographic variables in other habitat islands. Of course, the demographic states among habitat islands could be correlated because of a dependence upon some global environmental state, but there are no direct population-level interactions between habitat islands. Also, with no genetic interchange, evolution proceeds independently within each habitat island except for indirect correlations caused by global environmental conditions.

If the demographically fragmented demes are small in size, genetic drift becomes an important evolutionary force. Ultimately, genetic drift is expected to result in the loss of genetic variation. The rate at which this loss occurs depends upon the variance effective breeding size of the fragmented subpopulations. As can be seen from Figure 2, most glade populations of collared lizards show

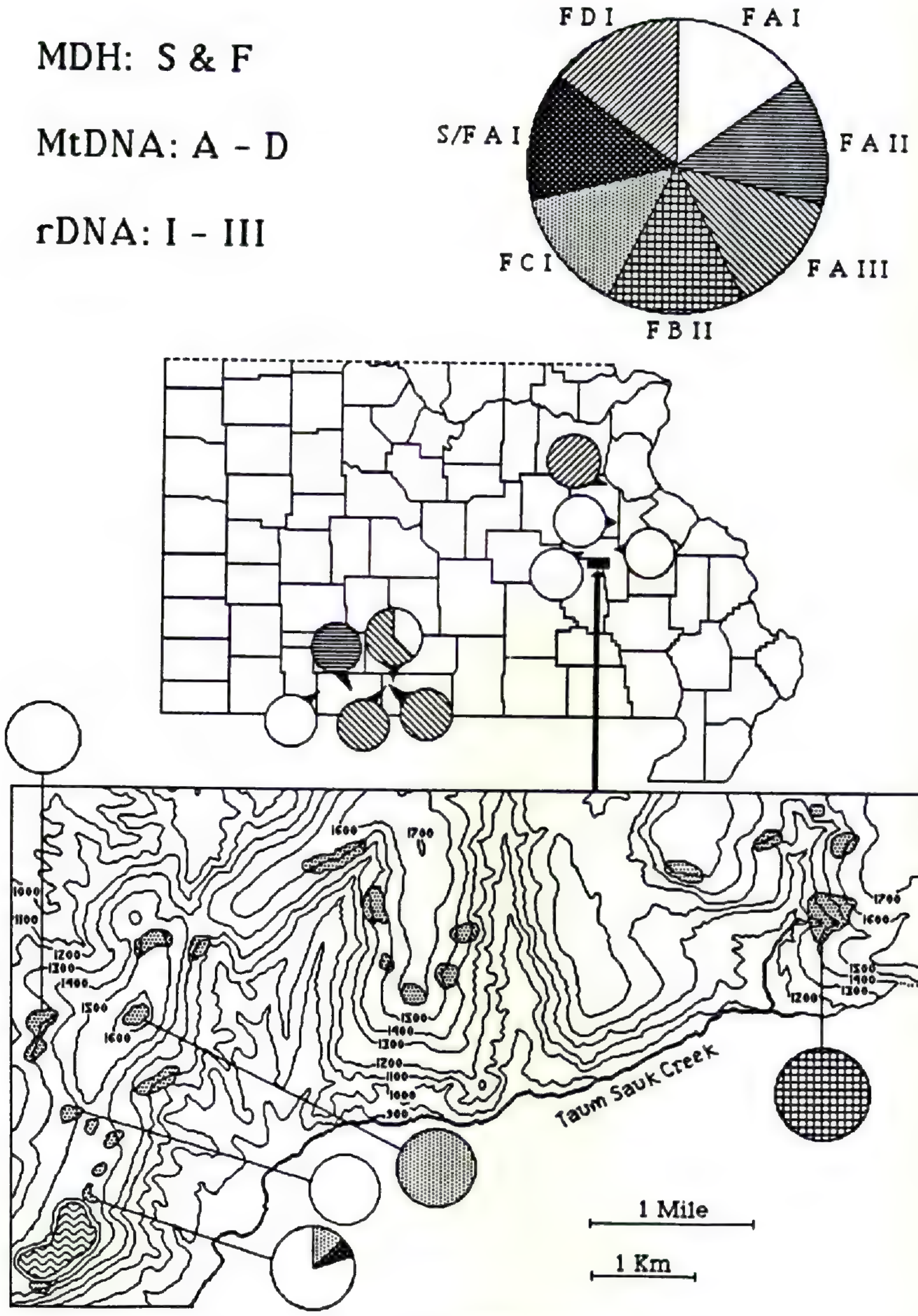

FIGURE 2. Distribution of isoyme, mtDNA, and rDNA genetic variants found in *Crotaphytus collaris*. A county outline map of the southern half of Missouri is shown, with pie diagrams indicating the genotype frequencies at various collecting sites from the data given in Table 3. An expanded scale map is shown of the area between Taum Sauk Mountain (on the far right of the expanded map) and Proffit Mountain (on the far left). Glades are indicated by stippled areas on this map. Contour intervals are 100 feet.

no polymorphism whatsoever. The only exceptions to this pattern are the Glade Top Trail populations, which were probably fragmented only very recently, and the population found on the parking lot near the Upper Taum Sauk Reservoir on Proffit Mountain. The reservoir has its walls reinforced by loose boulders, and this provides a dispersal corridor for lizards between previously isolated natural glades (indeed, lizards have been observed on these walls). Thus, this population is most likely an amalgam of previously isolated populations. Consequently, we conclude that most genetic variation in these lizards exists as fixed differences between glades rather than as polymorphisms within glades.

Unfortunately, these conclusions are tempered by the small sample sizes of several of these glade populations and by the relatively low levels of overall genetic variation. To obtain a more accurate quantification of the partitioning of genetic variation between and within glades, we performed an additional genetic survey using hypervariable VNTR loci on five glade populations having sample sizes between 4 and 58. We found a total of 13 variable, high-molecular-weight bands that could be reliably

TABLE 3. Results of various genetic surveys on *Crotaphytus collaris* populations found in Missouri glades and in central and western Oklahoma. The only polymorphic enzyme locus, malate dehydrogenase (MDH), had two alleles: "fast" (F) and "slow" (S). Four mtDNA haplotypes (designated A through D) were discovered, all due to length variation scorable with BclI digests. Four rDNA haplotypes were discovered as defined by the presence (+) or absence (−) of a PvuII restriction site and by length variants in the nontranscribed spacer detected by BamHI and by EcoRI. The most common haplotype is designated as I, and is coded as: −−− (i.e., it lacks the PvuII site, lacks the BamHI length variant, and lacks the EcoRI length variant). The other haplotypes are: II (+−−), III (++−), and IV (−−+).

Populations	Sample sizes	MDH	mtDNA	rDNA
Highway 21 Glade	3	F/F	D	I
Highway M Glade	2	F/F	A	I
Graniteville Quarry	1	F/F	A	I
Mina Sauk Glade	12	F/F	B	II
Proffit Mountain #4	1	F/F	A	I
Proffit Mountain #5	2	F/F	A	I
Proffit Mountain #7	2	F/F	C	I
Proffit Mountain parking lot	9	6: F/F	A	I
		2: F/F	C	I
		1: S/F	A	I
Glade Top Trail saddle	5	F/F	A	III
Glade Top Trail pinnacle	3	F/F	A	III
Glade Top Trail lookout	5	3: F/F	A	III
		2: F/F	A	I
Dewey Bald	2	F/F	A	II
Hercules Glade	2	F/F	A	I
Central Oklahoma	3	F/F	A	IV
Western Oklahoma	1	F/F	A	II

scored (there was obvious variation at some low-molecular-weight bands, but it was difficult to score). The results are summarized in Figure 3. As can be seen, a total of 25 different band phenotypes are observed, but only four of these phenotypes are found in more than one glade. We quantified the extent of partitioning of variation at the VNTR loci by estimating the proportion of shared bands within glades ($P_w = 0.74$) and between glades ($P_b = 0.50$). Moreover, we estimated the correlation of band phenotypes within glades relative to the total population to be 0.47. This correlation should be proportional to the standard F_{st} statistic (Rothman et al., 1974), which unfortunately cannot be estimated directly because the bands must be regarded only as phenotypes and not genotypes in the absence of information about number of VNTR loci and band homologies. However, this correlation will be greater than 0 only if F_{st} is greater than zero. This correlation of 0.47 is significantly different from 0 at the 1% level. Hence, F_{st} is also significantly different from 0 and rather large in value. Once again, we conclude that the majority of genetic variation is found as between-glade differences.

The fact that most genetic variation is found between glades not only confirms our conclusion that glades are demographically independent from one another, but it also implies that the variance effective breeding sizes within glades are very small. This inference is consistent with other data. The population on Sandy Ridge in Jefferson County seems to be one of the largest in the northeastern Ozarks. Yet the sample of 58 lizards constitutes a virtual census. Dr. Owen Sexton (pers. comm.) has followed this population in detail and has found that the adult population during the breeding season fluctuated between 21 and 79 individuals 1975–1985. Such small population sizes would cause a rapid partitioning of the ancestral genetic variation into the between-glade component.

These small population sizes imply that the glade populations should be very prone to local extinction. When populations are this small, inbreeding depression, environmental fluctuations, and demographic stochasticity can greatly increase the probability of local extinction (Quinn & Hastings, 1987). Given that there is no dispersal between glades, an "extinction ratchet" operates in which each local extinction brings the total population one step closer to global extinction. It is important to note that the rate at which this extinction ratchet operates is primarily a function of local, not global, population size. Hence, populations that are both

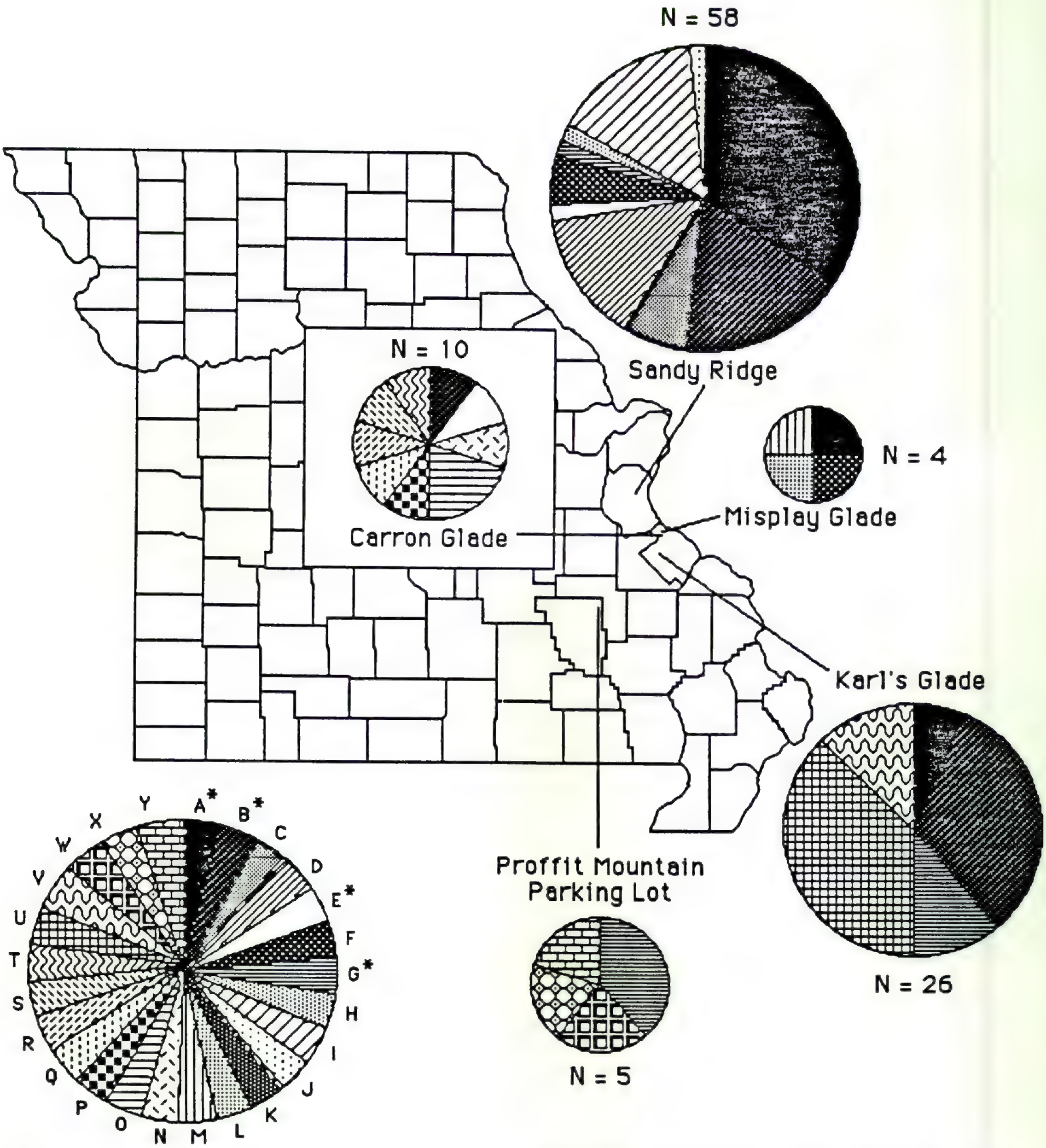

FIGURE 3. Distribution of hypervariable VNTR ("DNA fingerprinting") phenotypes found in *Crotaphytus collaris*. A county outline map of Missouri is shown, with pie diagrams indicating the phenotype frequencies in five glade populations. The number above, alongside, or below each pie diagram is the sample size from that glade. The DNA was cut with HaeIII and probed with the human fingergprinting clone 33.15.

fragmented and small should have a very high rate of local extinction and therefore high probabilities of global extinction.

There is much circumstantial evidence for local extinction in the lizards. The recorded county distribution for collared lizards in Missouri (Johnson, 1987) excludes many counties that have excellent glade habitat (Nelson & Ladd, 1981) and that are adjacent to counties known to have collared lizards. There is no apparent reason why the lizards should be absent from these counties, especially in view of the distributions of other glade-inhabiting animals and plants. Even within the counties known to have lizards, the authors have never observed collared lizards on many apparently suitable glades despite several trips to these glades and despite the fact that collared lizards are found on nearby glades. For example, Hawn State Park contains some sandstone glades that appear to be excellent habitat for collared lizards. Just outside the park are several

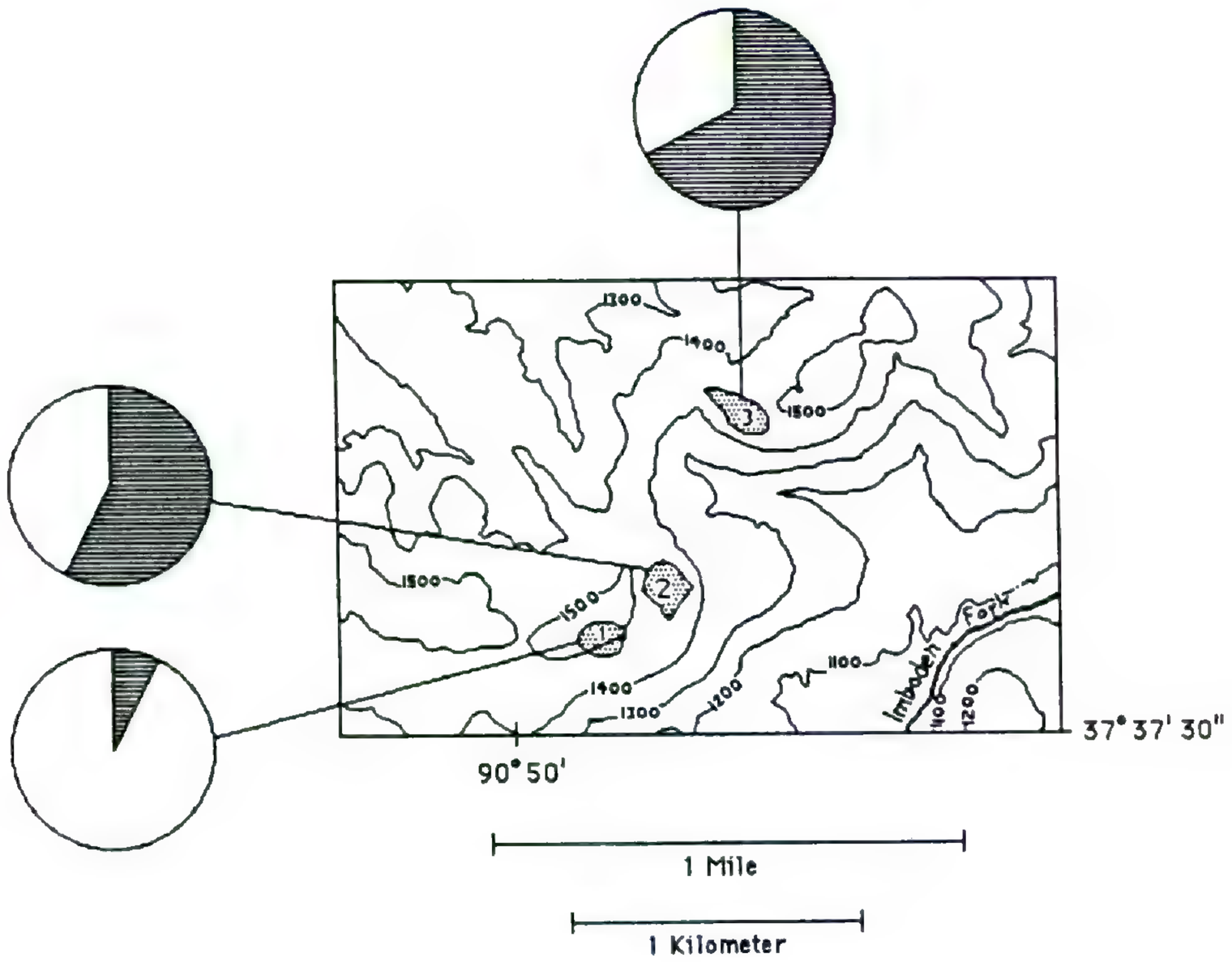

FIGURE 4. The frequencies of the alleles at the leucine aminopeptidase (LAP) locus in three glade populations of *Trimerotropis saxatalis* on Lindsey Mountain.

very healthy lizard populations, often on glades smaller than those in the park. Indeed, glades inhabited by lizards virtually surround the park. Yet there has never been a collared lizard recorded in the park, despite several deliberate surveys by knowledgeable people (Frank Crimmons, former superintendent of Hawn State Park, pers. comm.). This biogeographic pattern suggests that collared lizards have already undergone local extinction on many glades and is consistent with the inferences drawn from the genetic surveys.

As this example illustrates, genetic surveys with sufficient resolution to partition genetic variation between and within habitat islands can quickly identify those species at high risk for local extinction. The collared lizards are an example in which the genetic partitioning implies a high risk for local extinction. Our next example shows how genetic surveys can identify a fragmented species at a low risk for local extinction.

TRIMEROTROPIS SAXATALIS

Another glade inhabitant in the Ozarks is the lichen grasshopper, *Trimerotropis saxatalis*. This species is found primarily on glades with an acidic substrate, such as granite, rhyolite, or sandstone. We had difficulty performing an isozyme survey on this species because its proteins rapidly denature, but we did get good results for leucine aminopeptidase (LAP). Figure 4 shows the results of a survey of 16 individuals each (32 genomes) from three rhyolitic glade populations on Lindsey Mountain. There was no significant difference in allele frequency between glades 2 and 3, but there was between glades 1 vs. 2 or 3 despite the fact that glades 1 and 2 are only separated by about 150 yards of forest. This kind of genetic differentiation indicates that habitat fragmentation once again resulted in genetic isolation. Also note from Figure 4 that all three populations are polymorphic for the same LAP alleles. We are currently surveying for genetic variability in rDNA and mtDNA with restriction enzymes. Both DNA systems have revealed much genetic variation, but this variation has yet to be mapped. However, it is obvious from the Southern blot patterns that there is extensive polymorphism within all glade populations and that many variants are shared with other widely scattered glades—a pattern that is in great contrast to that observed for the collared lizards. Never-

TABLE 4. Distribution of mtDNA variants in four glade populations of *Trimerotropis saxatalis*. Cutting mtDNA with EcoRI yields five distinct patterns in these populations, labeled A–E.

	Glades			
Haplotypes	Sandy Ridge	Russell Mountain—2	Proffit Mountain—12	Steagle Mountain—7
A	2	3	3	0
B	4	3	6	6
C	0	0	0	2
D	1	3	0	1
E	0	2	0	0

theless, glade populations will frequently have at least some genetic variants not found in other nearby populations, which indicates absence of gene flow. For example, five distinct restriction fragment-length patterns are visible when the mtDNA is cut with EcoRI. Table 4 shows the number of individuals bearing these five haplotypes in four glades, and Figure 5 shows the geographical locations of these glades. As can be seen, all populations are polymorphic for mtDNA haplotypes, and most haplotypes are found throughout widely scattered areas. Yet, the Russell Mountain, glade 2 population has two mitochondrial haplotypes not found on the nearby (closer than 6 miles or 10 kilometers) Proffit Mountain, glade 12 population—a difference that is significant at the 1% level. Such a pattern is strongly indicative of no gene flow even between geographically close glades.

Although the lichen grasshoppers are highly fragmented into isolated glade populations, the large amount of within-glade polymorphism implies that the numbers within each glade are sufficiently large to insure that genetic drift is weak. This in turn implies that this species is in very little danger of local extinction except from environmental challenges that would cover the entire spatial scale of their habitat. This prediction is consistent with our collecting experiences for this species. Of 85 acidic glades visited that were a quarter of an acre or larger, these grasshoppers were found on all 85. In contrast, collared lizards were only observed on 14 of these 85 glades (however, some of these glades were only visited once, so it is probable that collared lizards are on more than 14 of them). These observations support the inference from the

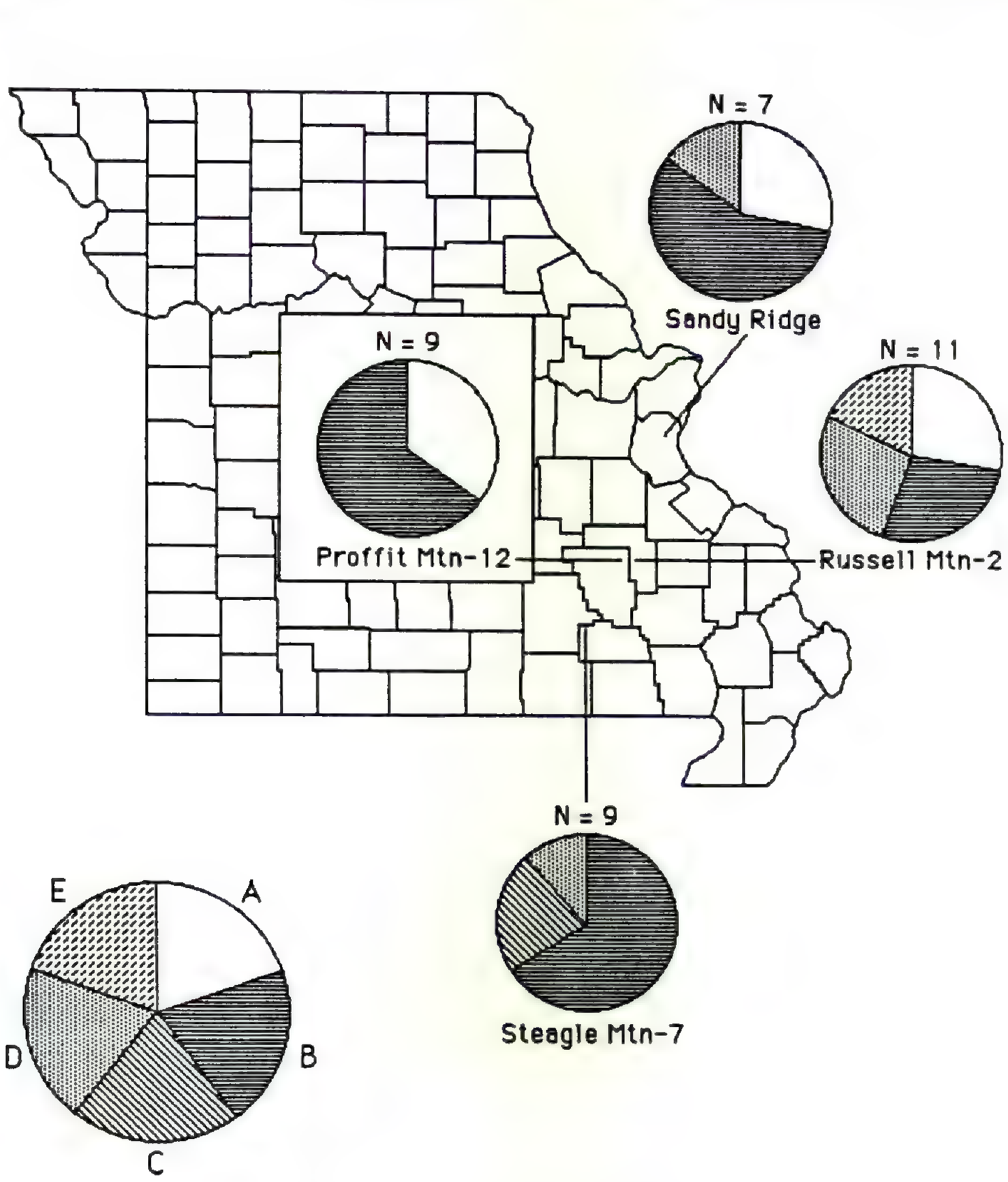

FIGURE 5. Distribution of mtDNA haplotypes found in *Trimerotropis saxatalis*. A county outline map of Missouri is shown, with pie diagrams indicating the haplotype frequencies in four glade populations. The number above each pie diagram is the sample size from that glade.

genetic data that the local populations of lichen grasshoppers are not at high risk for local extinction.

Management Recommendations

The ecological and genetic consequences of habitat fragmentation depend critically upon whether or not there is dispersal between habitat islands. The examples given in this paper show that genetic surveys are an extremely useful tool for addressing this critical question. The importance of genetic surveys is augmented further by the fact that it is not feasible to study dispersal directly for many species, but genetic surveys can be performed on virtually any species. Even when dispersal studies are feasible, genetic surveys are a more accurate means of inferring demographic fragmentation. For example, Lewis (1982) studied dispersal in the white-browed sparrow weaver, *Plocepasser mahali*. These birds are colonial breeders, and Lewis discovered that there is much successful immigration of dispersing birds into the smaller colonies. However, these colonies are not generally reproductively successful, and most birds in them are effectively dead genetically. Almost all successful reproduction is limited to large groups, and there is very little immigration into these. Hence, there is very little gene flow in this species despite much dispersal. On the other hand, basic population genetic theory (Crow & Kimura, 1970) shows that even very low dispersal rates—particularly, rare long-distance dispersal events—can be sufficient to maintain local populations as a single genetic unit. It is virtually impossible to estimate rare, long-distance dispersal rates in most species. Thus, genetic surveys provide a more reliable indicator of gene flow patterns than do dispersal studies. Genetic surveys are therefore a very powerful tool in identifying the pattern of demographic fragmentation caused by habitat fragmentation, and it is recommended that genetic surveys be utilized much more for this purpose.

Genetic surveys are also useful in identifying species at high risk for local extinction, given that demographic fragmentation has occurred. As illustrated by the contrast between collared lizards and lichen grasshoppers, we can make inferences about the long-term effective population sizes within habitat islands by partitioning the genetic variability into within-habitat-island and between-habitat-island components.

Species displaying small effective sizes are at most risk for inbreeding depression, demographic stochasticity, and extinction through environmental fluctuations. Many species that are endangered to begin with have low population sizes. Therefore, the most-endangered species suffer most from demographic fragmentation. Demographic fragmentation can therefore greatly accelerate the rate of extinction of an endangered species through the operation of the extinction ratchet. One obvious method of stopping the advance of the extinction ratchet is to recolonize artificially in order to counteract local extinction. In conjunction with the Missouri Conservation Commission, we have begun such a recolonization program for collared lizards in the Missouri Ozarks in order to study and monitor the success of various release strategies. Because the lizards are long-lived and the release program began in 1984, we do not have sufficient data to make evaluations. Nevertheless, our experiences in designing this release program have general implications.

One of the first decisions to be made is the goal of the release program. We feel that such release programs should preserve the genetic variability of the species while protecting it from extinction. With respect to genetic variation, there is a silver lining in the generally dark cloud of habitat fragmentation. As can be seen from the collared lizard example, when a population is fragmented into small, demographically independent isolates, there is rapid partitioning of the available genetic variation from within-habitat to between-habitat. The important point is that this is just a redistribution of the genetic variation, not its elimination. Genetic variation is still present as fixed differences between local populations. Moreover, population genetic theory (Maruyama, 1972) showed that global genetic variation is maintained more efficiently by a fragmented population than by a panmictic population, given an equal total size. The primary cause of loss of genetic variation in a finite population is genetic drift, but the genetic differences that are fixed between local populations can only be lost by extinction of the entire population.

Local extinction, however, can modify this prediction. As local extinction occurs, not only is population size reduced at the global level, but any unique genetic variants found in that local population are lost as well. As long as there are many local populations available, the loss in global genetic variation caused by local extinction is very little. But as the extinction ratchet decreases the number of local populations, genetic variation loss will accelerate. Accordingly, recolonization intervention is needed to prevent extinction and to insure that a sufficient number of local populations are maintained so that global genetic variation can be preserved. However, the goal of preserving genetic

variation places constraints on how the recolonization should be done.

There are two basic strategies in a recolonization program. One strategy is to obtain all the animals for a release from a single, local, large population. The alternative is to obtain the release animals from several local populations and recolonize with a mixed population. Arguments can be made for both strategies.

With a mixed release, high levels of genetic variability can be reestablished at the local population level. However, since the released population will in general be small, this variation will be rapidly lost due to genetic drift. Nevertheless, even a temporary infusion of genetic variability into the local population can be beneficial. Evolution within the local population can occur only if there is genetic variability, so natural selection in the local population is possible for the first few generations after the release of a mixed population. Hence, a mixed release allows some adaptation to the local environment. This could be important in increasing the chances of success of the released population if the environment in which the release takes place is not identical to the environments experienced by the source populations.

Local adaptation could, however, sometimes favor the strategy of nonmixed release. Frequently, local adaptation in small, isolated populations is achieved by the accumulation of "coadapted" gene complexes (Templeton, 1986). Even populations adapting to the same environment will often achieve that adaptation in genetically distinct and incompatible fashions. When these coadapted complexes are broken down by recombination, the average fitness of the population could be lowered dramatically—a phenomenon known as "outbreeding depression" (Templeton, 1986; Templeton et al., 1986). If severe enough, an outbreeding depression could greatly increase the chances of extinction of the released populations.

Annest & Templeton (1978) have experimentally monitored the evolutionary and ecological significance of outbreeding depression in *Drosophila* populations. They showed that the lowest population sizes occur during the first generation in which recombination can break up coadapted complexes (generally, the F_2 or backcross generations). Therefore, extinction due to outbreeding depression generally will occur in the first few generations after release. After that, selection operates to reestablish one of the parental coadapted gene complexes or evolve a new one. In either case, the absolute fitness increases and population size rises. Annest & Templeton (1978) found that when a new coadapted complex arose, it generally had superior fitness traits to any of the input parental complexes. Thus, if the population can survive the first few generations, the outbreeding depression will be eliminated by the action of natural selection and it is possible that the surviving population will have higher fitness than any parental population. Consequently, even if there is an outbreeding depression, mixed releases still might be best in the long run. It would be essential to monitor the released populations closely for at least the first three to five generations. For example, we obtain a blood sample from all collared lizards before release to provide genetic markers to detect outbreeding and/or inbreeding depressions. These genetic markers will also allow us to estimate accurately the variance and inbreeding effective sizes of the released populations by observing the rate of decay of genetic variation through time. If severe outbreeding depressions occur, the mixed release strategy might have to be abandoned to insure the survival of the populations in the recolonized areas.

In addition to outbreeding depression, the released population may suffer from inbreeding depression. Inbreeding depression is usually caused by the increased incidence of homozygosity for recessive deleterious alleles that occurs with inbreeding. Inbreeding and outbreeding depression are not mutually exclusive since they can involve different genetic systems found in the same organisms. When inbreeding occurs because of small population size, deleterious alleles have a finite chance of going to fixation. Hence, the real danger in small, isolated populations is that the inbreeding depression will be fixed by genetic drift. O'Brien et al. (1985) have argued that such a fixed inbreeding depression may account for the low reproductive performances of cheetahs. Fixed inbreeding depressions represent a serious problem for the survival of local populations and for the species. We would expect the local populations displaying the most severe inbreeding depressions to go extinct more rapidly. Therefore, as time proceeds, the average severity of fixed inbreeding depression should decrease, but over even long periods of time, we expect fixed inbreeding depression to rise again. When population sizes are very small, even deleterious mutations have a finite chance of fixation (Crow & Kimura, 1970), and once fixed, there is no mechanism to purge the deleterious mutation from the local populations under complete genetic isolation. This results in a situation analogous to "Muller's ratchet" in which deleterious alleles will tend to accumulate until the population is driven to extinction (Muller, 1964).

By carrying out a mixed release, the temporary infusion of heterozygosity will alleviate the inbreeding depression for the first few generations after release. As the generations progress, inbreeding will become reestablished in the released populations, and hence inbreeding depression may reappear. However, just as outbreeding depressions can be eliminated by the operation of natural selection, so too can inbreeding depressions (Templeton & Read, 1983, 1984). With a mixed release, natural selection has a renewed opportunity to eliminate deleterious alleles. Random drift may once again cause fixation of deleterious genes, but natural selection biases the stochastic fixation process against that possibility. Also, this temporary influx of genetic variation allows recombination to be effective at producing new genotypes, and this recombination can help undo the damage done by "Muller's ratchet" (Muller, 1964). By releasing from a single source population, there is no opportunity for selection or effective recombination to operate, and therefore any fixed inbreeding depression in the source populations will remain fixed and "Muller's ratchet" will proceed unabated.

The benefits from selective processes operating in released populations increase as the initial amount of genetic variation increases. Accordingly, the best mixed release strategy combines individual populations from a large number of habitat islands. The selective benefits also increase as the number of generations with genetic variation after release increases. The number of genetically variable generations can be maximized by making the released population as close as is practical to the ultimate carrying capacity of the habitat island to be recolonized.

Mixed releases also aid in the goal of preserving overall genetic variability. When all individuals for release are drawn from a single source population, it is essential that the source population be very large so that harvesting individuals from it will not endanger the source as well. Such large releases reduce the chances of extinction and increase the opportunity for natural selection to promote local adaptation and eliminate outbreeding and inbreeding depressions. Only a few source populations will be sufficiently numerous to support this extensive harvesting. For example, we have identified only four glades that could support a harvesting of 10 collared lizards—our minimum release size—without seriously endangering the survival of the source population. As the collared lizard example shows, the released populations under the single source strategy will often be genetic clones of a small number of source populations. Thus, genetic variation at the global level will be rapidly depleted under this recolonization strategy.

In contrast, the multiple-source recolonization strategy can preserve large amounts of global genetic variation. First, because only a few individuals need be taken from any single local population, many more local populations can qualify as source populations, as illustrated by our collared lizard release program. By doing mixed releases in which all animals come from different glades, we need only harvest a single animal from any particular glade. Virtually all natural populations can endure that level of harvesting without ill effect. The recolonization program this way can tap into much more of the global genetic variability contained in the fragmented species. After release, genetic drift will cause loss of variation. However, different releases will undoubtedly become fixed for a different array of genetic variants. Hence, there will be no tendency to "clone" a handful of source populations; instead, the released populations will be genetically diverse relative to one another and to their sources. In this manner, very high levels of global genetic variation can be maintained in the fragmented species despite high rates of local extinction. Follow-up monitoring of the released populations is just as important as the initial release in order to insure that genetic diversity is being preserved and to check for the possibility of outbreeding depressions.

Summary of Recommendations

Genetic surveys are an extremely powerful tool for identifying demographically independent habitat islands and should be used more extensively to infer the pattern of genetic fragmentation. Indeed, genetic surveys offer a more reliable means of inferring demographic fragmentation than dispersal studies and can be applied easily to a wide diversity of organisms.

Second, genetic surveys, particularly those utilizing high-resolution techniques, such as DNA fingerprinting, can be used to spot fragmented species at high risk for local extinction. This is accomplished by quantifying the partitioning of genetic variation between and within demographically independent habitat islands.

For species with a high risk of local extinction, recolonization programs are needed to protect the fragmented species against global extinction and to preserve its pool of genetic diversity. In general, a mixed release strategy is best, with the numbers to be released ideally as close as possible to the carrying capacity. Released populations must be

monitored genetically and demographically for the first few generations after release to detect potential inbreeding and/or outbreeding depression and periodically thereafter to insure that genetic diversity is indeed being preserved.

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CONSERVING BIODIVERSITY IN THE CANARY ISLANDS

David Bramwell[1]

Abstract

The flora of the Canary Islands is rich in endemic species and shows typical insular evolutionary features, such as large-scale adaptive radiation (*Echium, Sonchus, Argyranthemum, Aeonium*) and interisland vicariance. It is also a relict flora of the Tertiary Epoch of the Mediterranean Region and the drier regions of Africa, and as such has enormous scientific value. Many taxa (e.g., *Olea europaea* subsp. *cerasiformis, Brassica bourgaei*) are valuable economic plants or close relatives whose conservation is of considerable importance. Locally, action has been taken on various levels to provide protection, especially for natural areas. This involves major legislation (Ley de Espacios Naturales), planning via a series of "Planes Especiales para Protección de Espacios Naturales," and establishment of national parks, biosphere reserves, and a World Heritage Site. This is supported by intensive research on endangered species involving studies of genetic diversity, population biology, breeding systems, resource evaluation, micropropagation, and restoration of some ecosystems. Some of the theoretical and practical difficulties encountered in this field are noted. The role of local botanical gardens in planning, conservation-oriented research, and the extremely important field of environmental education is explained, and the value of the garden as the interface between ex situ and in situ conservation is considered.

Since the middle of last century, when Charles Darwin published the remarkable conclusions drawn partly from his observations on the fauna and flora of the Galápagos Archipelago, islands have fascinated scientists because they are natural biological and evolutionary laboratories where evolution in isolation has permitted the survival of rare, relict endemic taxa and at the same time promoted the formation of new, often equally rare and interesting ones.

Islands, therefore, can provide a novel and invaluable scientific resource. Particularly when we are concerned with the conservation of small populations and the protection of very rare species, there are many theoretical and practical conservation lessons to be learned from island systems. This is especially true for the fields of population genetics and behavior.

Recent research, such as that carried out on Hawaiian organisms during IBP (International Biological Program) "Integrated Island Ecosystems Program," suggests that, contrary to widespread popular belief, the genetic properties of island populations are essentially similar to those of continental ones (see Carson, 1981, for full discussion of this subject). This is confirmed by work on Canarian groups, such as *Lotus*, where the range of karyotype variation and cyanogenic properties closely parallels that reported from continental European species (Ortega, 1978; Urbanska & Willdi, 1975). Thus, concepts derived from the study of the behavior of small isolated populations from islands should be even more applicable to rare and endangered continental species than suspected before the IBP research.

Islands, however, are very vulnerable to ecological change, especially the disruptive and destructive alteration brought about by human interference in insular ecosystems, the direct effects of humans and those of domestic animals and plants as well as their camp followers, weeds and pests. The *IUCN Plants Red Data Book* or the recently published *Plants in Danger: What Do We Know?* (Davis et al., 1986) reveal how many ecosystems and species are currently threatened on islands (Table 1).

Biodiversity in the Canary Islands

From the islands conservation point of view, the Canaries are no exception. The archipelago of seven main islands and several small islets and rocks covers over 7,250 km^2 with a population of some 1.5 million (approximately 206 people per km^2). The total flora, which is taxonomically well known, is about 2,000 species with just over 500 endemics, i.e., 25% endemism. The total figure, however, includes a number of weeds and aliens. Endemism is probably between 35% and 45% of the native flora. For such a small area, this is a remarkable

[1] Jardín Botánico "Viera y Clavijo," Excmo. Cabildo Insular de Gran Canaria.

TABLE 1. Small oceanic islands with devastated floras. Ex extinct, E endangered, V vulnerable, R rare, I indeterminate, K insufficiently known, nt not threatened.

	Ex	E	V	R	I	K	nt	Total	Rare or threatened
Ascension Island	1	5	–	4	–	1	–	11	10 (91%)
Bermuda	3	4	1	6	–	?	?	?	14
Norfolk Island	5	11	29	–	1	2	–	48	46 (96%)
Rodrigues	10	20	8	8	–	–	2	48	46 (96%)
St. Helena	7	23	–	17	–	2	–	49	47 (96%)

degree of diversity and endemism. The total flora is larger than that of the British Isles, where the area is almost 34 times that of the Canary Islands.

Although over 67% (383) of the endemic species are rare, threatened, or endangered (Fig. 1), most are extremely tenacious and capable of hanging on in precarious circumstances over long periods. Since the first relatively comprehensive accounts of the flora were published last century (Webb & Berthelot, 1836–1850; Sauer, 1880) only a single species, *Solanum nava*, has not been found again during the last 20 years. Areas of good natural vegetation, on the other hand, have been decimated over the past 500 years and especially in recent decades.

The flora of the Canary Islands is of particular interest for a number of reasons, and the arguments for its conservation are scientifically and economically strong.

Paleobotanical and biogeographical data suggest that it is historically a relict flora (Bramwell, 1972, 1976, 1985). Its closest relatives are in either the Tethyan–Tertiary Region along the edges of the Tethys Sea, principally in the late Miocene and Pliocene periods, or along the drier margins of eastern and southern Africa, the Arabian Peninsula, and Socotra as a relict of a once more widespread semidesert flora of the pre-Holocene (Quezel, 1978; Bramwell, 1985). The islands are now isolated from their main source areas by time, by sea, and by desert. This has resulted in a postisolation phase of evolution with adaptive radiation and vicariance leading to two main types of endemic taxa: the relicts that have not undergone speciation on a large scale (*Dracaena*, *Bosea*), and the active epibiotics (Bramwell, 1972), which at the generic level are probably relicts (*Aeonium* found in Macaronesia and East Africa, for example) but have a plethora of local endemic species due to adaptive radiation. In fact, in *Echium*, *Sonchus*, *Argyranthemum*, and *Aeonium*, we have some of the finest examples of plant adaptive radiation on islands anywhere (Lems, 1960; Bramwell, 1972, 1975; Humphries, 1976; Aldridge, 1979). These evolutionary models merit conservation in as complete a state as possible since every species that becomes extinct breaks a link in the chain and makes our understanding of the processes, patterns, and products of their evolution more difficult.

Many of these Canarian endemics survive in very small populations and have, according to the literature, done so for over a century (Cabrera y Diaz, 1910) so that there may be much to learn from their genetics, population structure, and the roles of dormant individuals held in the natural seed reservoir in maintaining long-term variability and fitness. This, coupled with the scientific interest of the flora, is a valid reason for conservation of such model floras.

There are, however, other reasons for concern for the conservation of the Canarian flora. Because

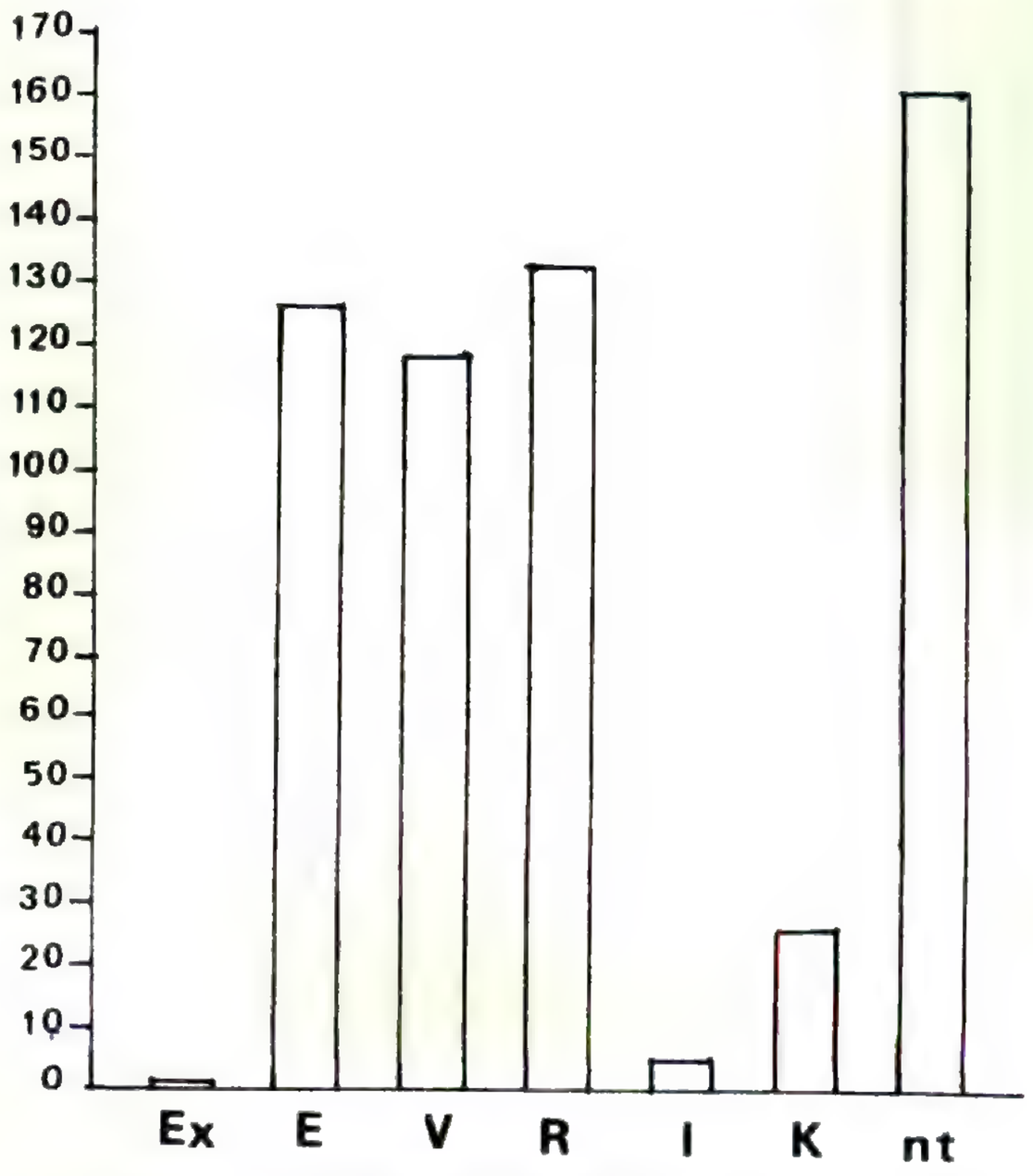

FIGURE 1. Threatened endemic plant species of the Canary Islands assigned to IUCN Categories. Ex extinct, E endangered, V vulnerable, R rare, I indeterminate, K insufficiently known, nt not threatened.

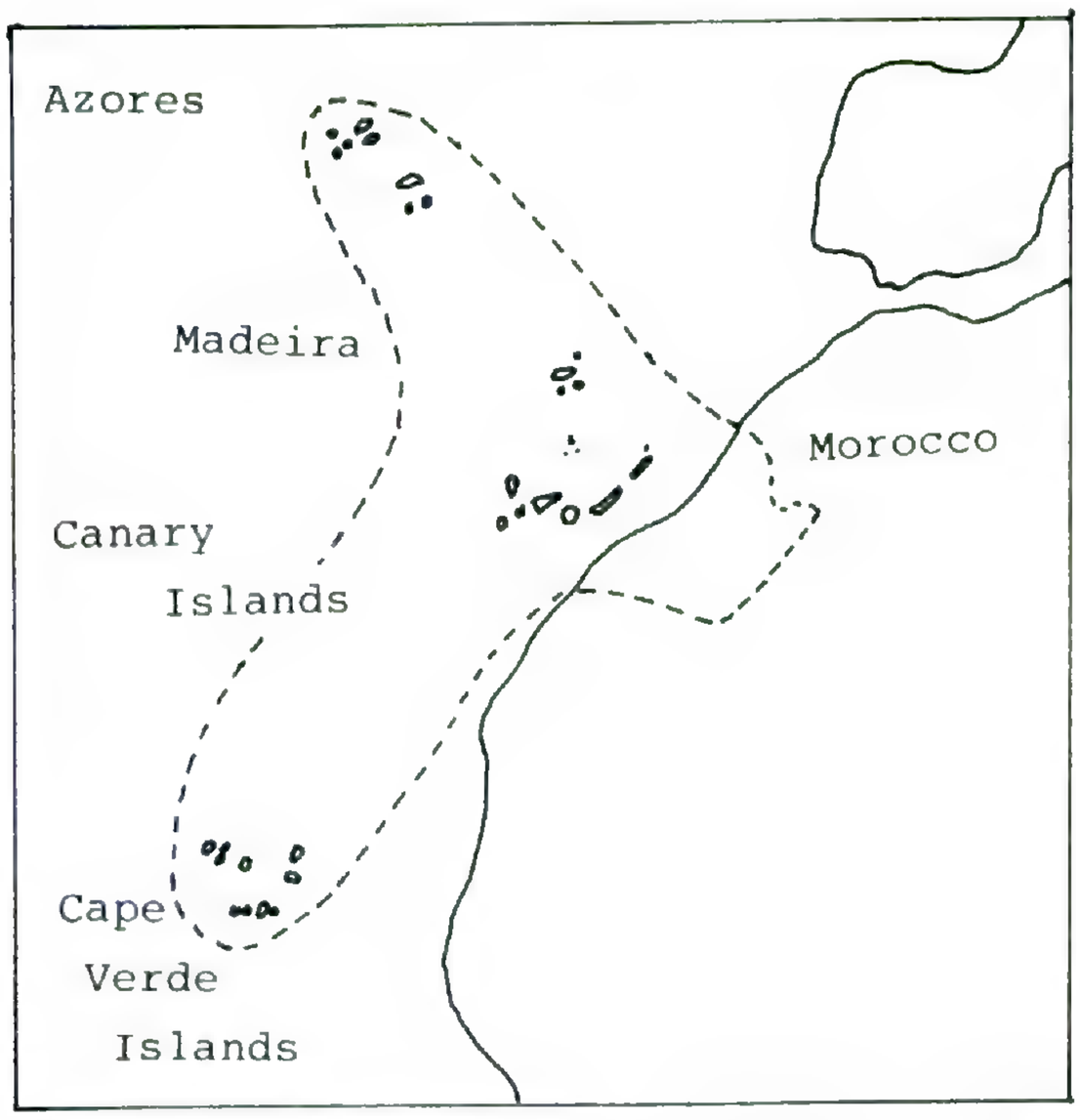

FIGURE 2. The geographical situation of the Canary Islands. — Limit of the Macaronesian Region.

of its historical association with the old Mediterranean floras of the Tethyan–Tertiary, the Canarian flora has a number of wild relatives of classical Mediterranean economic plants and crops; among the most important of these are *Olea europaea* subsp. *cerasiformis*, *Phoenix canariensis*, *Brassica bourgaei*, *Cytisus proliferus*, *Beta webbiana*, *Avena canariensis*, and *Dactylis smithii*.

To species such as these we can add a long list of potentially valuable ornamental species in such genera as *Argyranthemum*, *Limonium*, *Lotus*, and *Senecio* sect. *Pericallis* (endemic to Macaronesia and with the vast majority of species local endemics in the Canaries) which is the Florist's Cineraria. there are also many local medicinal uses for endemic species but, although some of these have been the subject of a recent review (Perez de Paz & Medina, 1988), their active constituents have not in most cases been studied in detail.

The major vegetation types and plant communities of the islands are endemic to the Canaries or in some cases to the Macaronesian Region (Fig. 2). These include a *Euphorbia* scrub zone (dominated by *Euphorbia broussonetii*, *E. aphylla*, *E. canariensis*, and other species), which is similar to some North and East African communities; the humid laurel forests in which all the dominant trees are endemic to the Macaronesian Region and are relicts of the Tethyan–Tertiary Region of approximately 4 million years ago; montane forests of the locally endemic pine, *Pinus canariensis*, which has its nearest relatives as Tertiary Mediterranean fossils and as the extant species *P. roxburghii* in the West Himalayas. The subalpine zone of the islands occurs only on Tenerife and La Palma and has over 90% endemism among the perennial plants; it shows morphological and physiological similarities to the Afro-Alpine zone of East Africa.

Conservation Problems in the Canary Islands

Before the Spanish occupation in the fifteenth century, the Canary Islands were inhabited by a people, variously known as Guanches or Canarios, with a relatively simple neolithic culture who seem to have lived in relative harmony with their natural environment. After the fifteenth century, however, the situation changed considerably, especially when sugar cane was introduced to the islands and large areas of land were cleared for its cultivation. Forests were cut down to provide space and to fuel the sugar extraction and refining. As Ayensu et al. (1984) pointed out, "The natural vegetation of these islands was further affected, often totally destroyed, by the cultivation of tomatoes and grapevines, the terracing of the slopes for these and other vegetable crops, the widespread cultivation of bananas in coastal zones, and the introduction and spread of many Mediterranean weeds. This all led to a lowering of the water table and increased aridity." This proceeded over 500 years to such an extent that the laurel forest of Gran Canaria now covers less than 1% of its original area (Fig. 3) and on the island of Tenerife, less than 10% of its former extent.

From this brief summary of the recent history of the environment in the islands we can see that the main destructive force has been humans through pressure of land use and the destruction of natural resources, but in the second half of the twentieth century a further phase of deterioration is under way due to the massive expansion of tourism in the islands.

Large-scale tourist development (200,000 tourist beds on the island of Gran Canaria alone) brings with it enormous environmental problems. The pressure on coastal region land resources, the constant need for building materials, the strain on local water resources, coastal pollution and disposal of domestic rubbish, and even the damage caused to natural areas by recreational off-road vehicles probably pose the biggest threats to biodiversity and natural resources ever. One of the major, but little-considered, impacts is homogenization of the habitat, the destruction of ecologically well-defined vegetation zones, which leads to species swamping by hybridization (see Brochmann, 1984, for further discussion) and continuously tends toward environmental uniformity and away from diversity.

Faced with such negative effects of human intervention in the environment, the need for an equally interventionist and positive conservation program is obvious.

ENVIRONMENTAL CONSERVATION IN THE CANARY ISLANDS

Conservation in such circumstances is necessarily a multifaceted activity with the following fields of action: legislation (protection of areas, protection of species), planning, research, and education.

Legislation

Protection of the environment is provided for in Spanish law at various levels, from the Constitution to the 1975 Laws on Protected Natural Areas under which the Spanish National Parks were consolidated, and under minor parts of several other national laws on, for example, hunting, mining and mineral extraction, forestry, and water resources. The autonomous regional governments in Spain also have the powers to legislate locally on environmental matters.

National legislation, at least in theory, protects some species. The hunting laws (Ley de Caza art. 23.2, 1970), for example, state that "Species of scientific interest or in danger of extinction will be the subject of special protection . . . ." and under this legislation a royal decree (3181/1980) lists nationally protected species and includes most of the native birds, reptiles, and amphibians of the Canary Islands.

Following Spain's ratification of the Berne and Bonn conventions on the environment and migratory species of wild animals, respectively, many more migratory and visiting birds were added to the list of protected species.

Plant conservation legislation is, however, at individual species level rather less developed and is based mainly on forestry legislation and a series of royal decrees protecting tree species. It does cover the majority of laurel forest species but has proven to be difficult to apply to private landowners. Spanish law does envisage the protection of individual species, and for mainland Spain and the Balearic Islands two decrees from 1982 and 1984 give protection to some wild endemic plants. In the Canary Islands, however, we do not yet have any legislation specifically protecting species other than the forest trees already mentioned.

We have recently prepared a proposed protected species list (Bramwell & Rodrigo, 1982) and this year updated it at the request of the Environmental Department of the Regional Canarian Government with a view to preparing new local legislation for the protection of Canarian endemic plants; we hope that this will take effect during the next 12 months. Draft legislation for a new comprehensive law on environmental protection is also being prepared at the moment, and in 1987 a law was passed placing most of the major areas of conservation importance in the islands in a catalog of protected natural areas (Fig. 4). These cataloged areas are now pending the preparation of individual use and management plans, which is the responsibility of the Dirección General de Medio-Ambiente (Directorate General of the Environment).

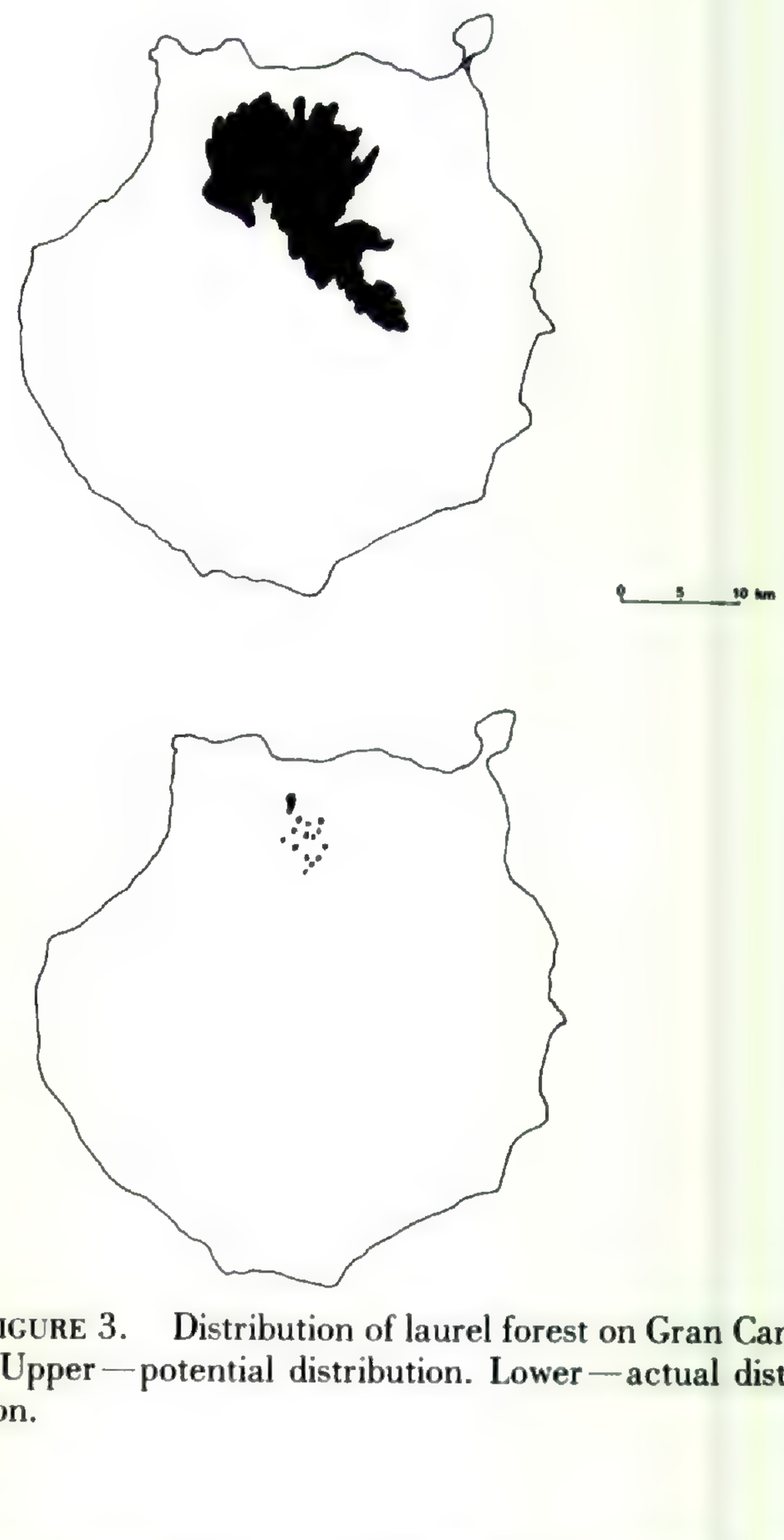

FIGURE 3. Distribution of laurel forest on Gran Canaria. Upper—potential distribution. Lower—actual distribution.

Existing law has been put to good use in the Canaries at two levels, both concerned mainly with in situ ecosystem protection.

At the first level, the international conventions on World Heritage Sites and Man and the Biosphere Reserves have been used to conserve two of the best areas of Canarian laurel forest, El Cedro-Garajonay on La Gomera (Fig. 5), which is also a national park, and Monte del Canal on the island of La Palma. The Canary Islands have four national parks, the subalpine zone of Tenerife (Parque Na-

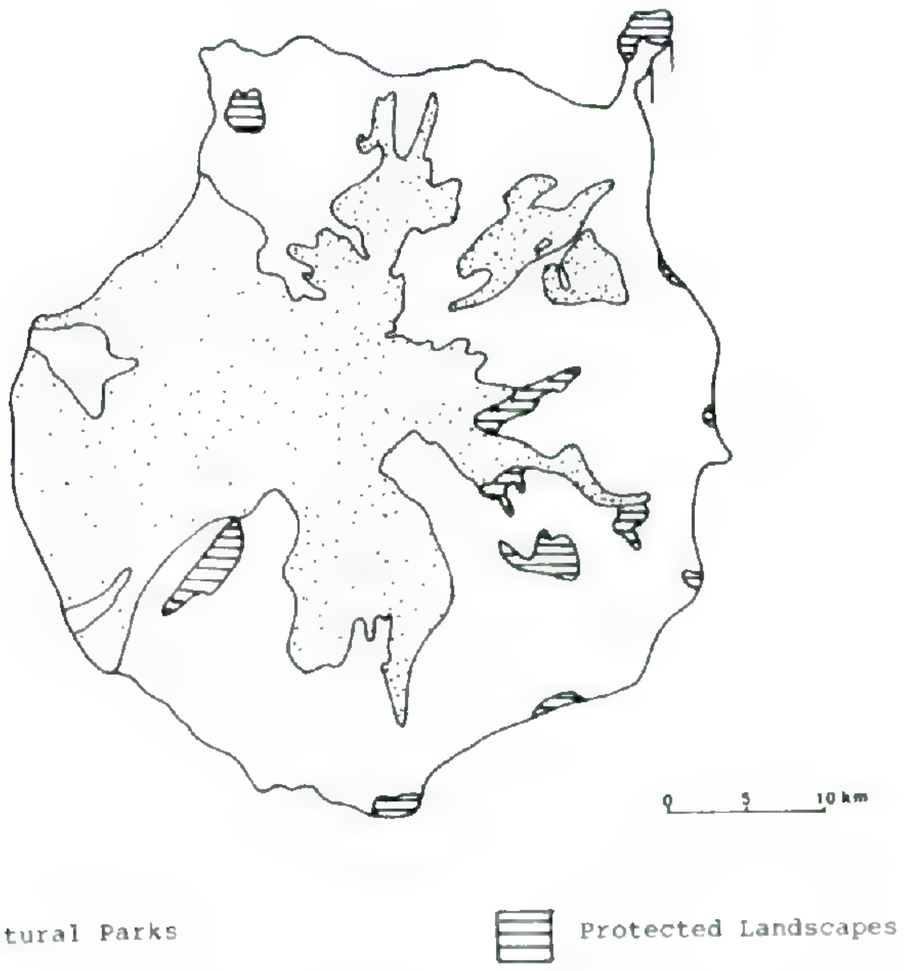

FIGURE 4. Protected areas of Gran Canaria included in the Ley de Espacios Naturales of the Autonomous Regional Government (1987). Dots—natural parks. Lines—protected landscapes.

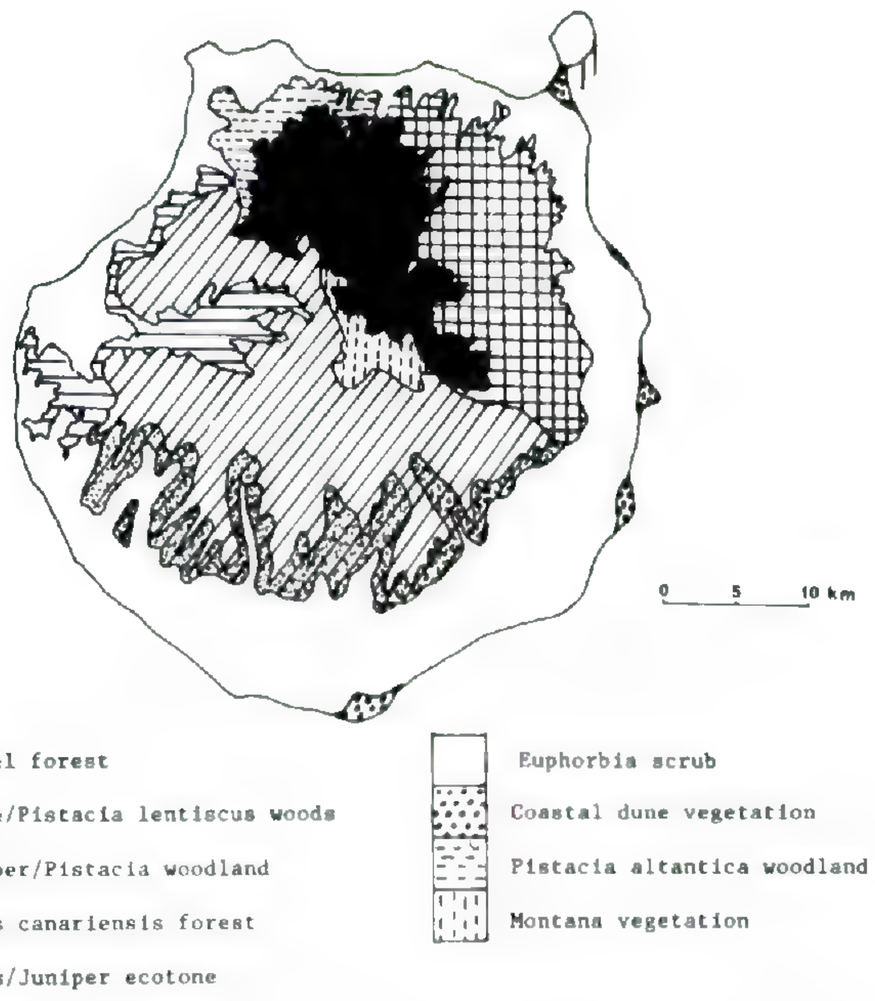

FIGURE 6. The potential natural vegetation of Gran Canaria.

cional del Teide) covering 13,500 hectares; Parque Nacional de La Caldera de Taburiente on La Palma, which is a pine forest park of 4,690 hectares (ha); the volcano park on Lanzarote (Parque Nacional de Timanfaya) with 5,107 ha; and the already mentioned Parque Nacional de Garajonay with an area of 3,950 ha mainly of laurel forest.

The second level of action in the Canaries has been promoted by the Autonomous Government and the local individual island councils (Cabildos Insulares). Taking advantage of Spanish Town and Country and Country planning law (Ley de Suelos), a series of planning projects classifying land has been undertaken for each island. I explain the one for Gran Canaria in detail as a possible example of the use of planning legislation for natural ecosystem protection on islands.

Planning

Often the philosophy behind the designation of national parks and nature reserves is "monumentalist" so that great landscapes and so-called wild areas are given priority, and this was certainly true for the original national parks of the Canary Islands, those of Teide, Taburiente, and Timanfaya. These three parks protect only a very small proportion of endangered Canarian endemic species. This was a particular problem for Gran Canaria in the center of the archipelago because it had no national park and very few protected areas in 1983 when the Jardin Botanico "Viera y Clavijo" was asked by the Canarian government and the Cabildo Insular de Gran Canaria to form an interdisciplinary team of biologists, geographers, lawyers, and architects to prepare a special plan for the protection of natural areas under Spanish planning law. The methodology we used was to take a wholly scientific approach to the problem and study the entire island rather than to rely on preconceived ideas about which areas of the island should be protected. In part this was done because previous attempts to delimit natural reserves had failed to protect sufficient areas because they did not consider restoration of degraded areas as a viable conservation policy. A summary of our study of the island has already been published (Bramwell et al., 1986), and I give a brief outline of it here.

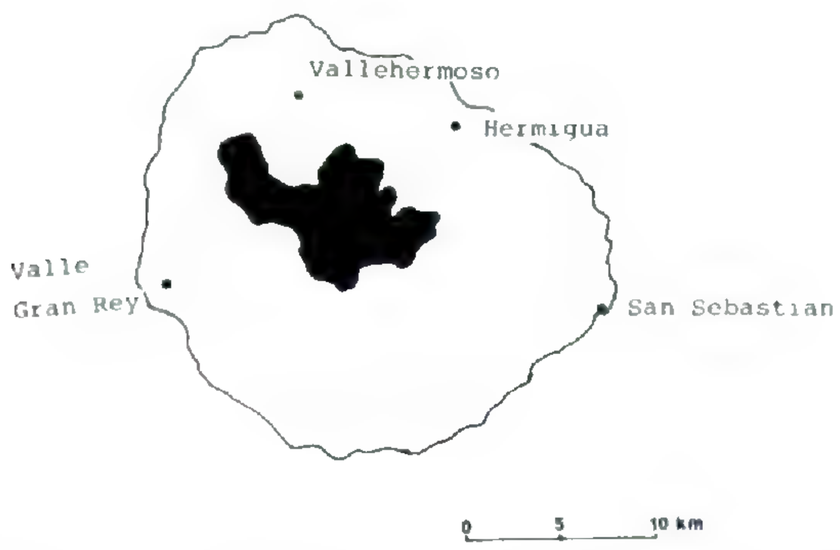

FIGURE 5. National Park of Garajonay, La Gomera, recently accorded the status of World Heritage Site.

The first phase of preparation involved a review of existing information, bibliography, and the experience of members of the team (which was an important source of data). This enabled us to build up a picture of the island leading to the identification of major gaps in our knowledge, some of which were then worked on by the team, and others through the cooperation of outside specialists. The following studies made important contributions to the project:

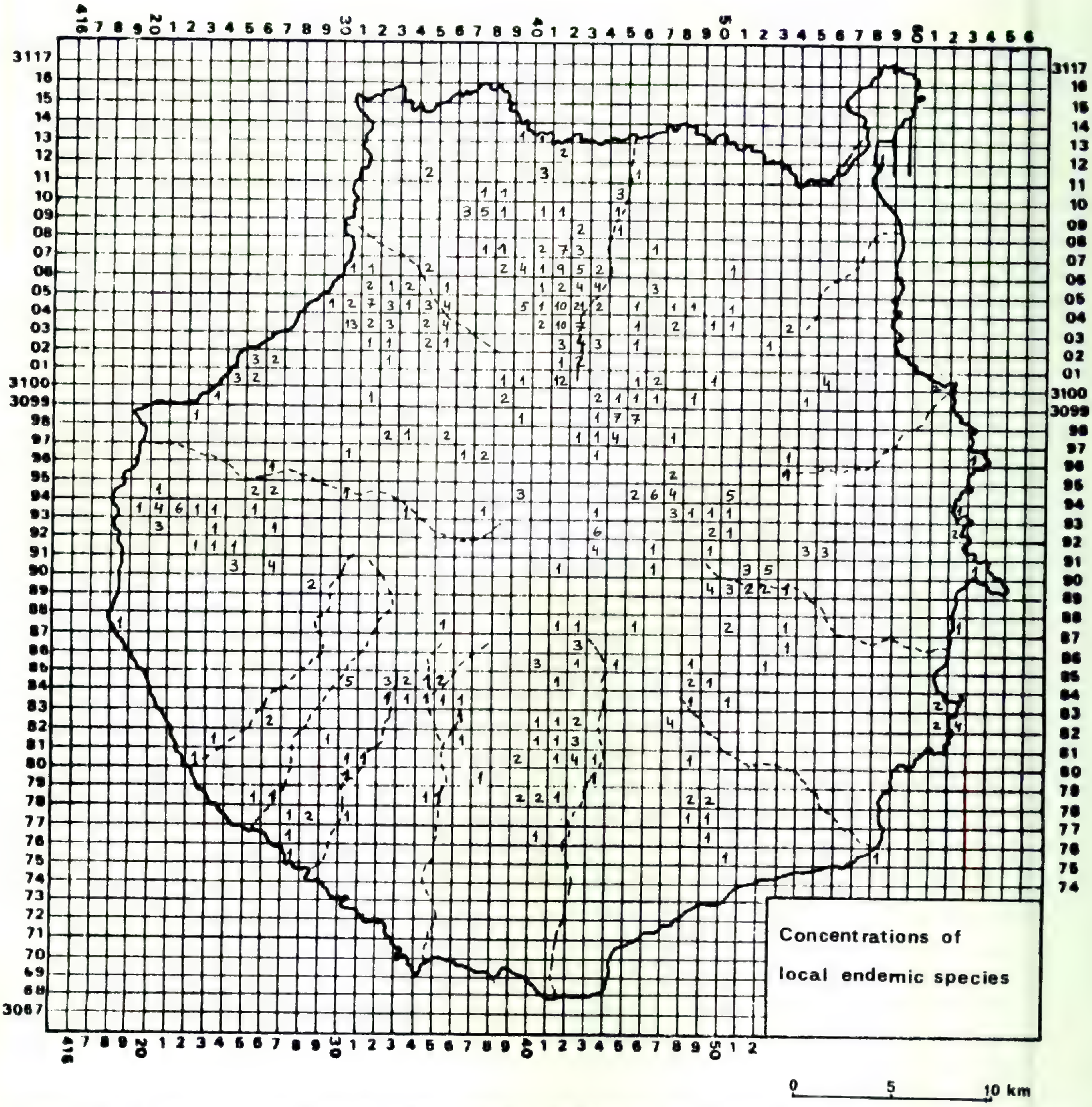

FIGURE 7. The distribution of local endemic species; figures indicate the number of Gran Canarian endemics per km².

1. Existing land use. 2. Population distribution. 3. Geomorphological features, mining, and mineral extraction. 4. Areas of ornithological interest. 5. Distribution of native vertebrates. 6. Entomology. 7. Potential (Fig. 6) and actual natural vegetation. 8. Rainfall and water resources. 9. Areas of archaeological interest. 10. Existing town and country planning. 11. Tourist development. 12. Distributions of rare endemic species (Fig. 7).

Only when all this information had been analyzed did we preselect areas that were then subjected to intensive field studies and ranked according to their value as potential protected areas. As a result, and in order to avoid creating what McEwen & McEwen (1982) described as "islets of natural beauty . . . in a sea of destructive practises," we decided it was necessary to give at least some protection to very large areas even though the number of zones needing absolute protection was relatively low.

After detailed mapping of boundaries using aerial photographs, the final number of protected areas was 64, varying in size from 0.5 ha to 14,478 ha and totalling 109,574 ha or approximately 60% of the area of the island (Fig. 8); these protect the main populations of all the endemic plant species as well as the vast majority of birds, reptiles, and insects. The levels of protection proposed are indicated in Bramwell et al. (1986). The Plan Especial has been provisionally approved by the Cabildo Insular de Gran Canaria and has been passed

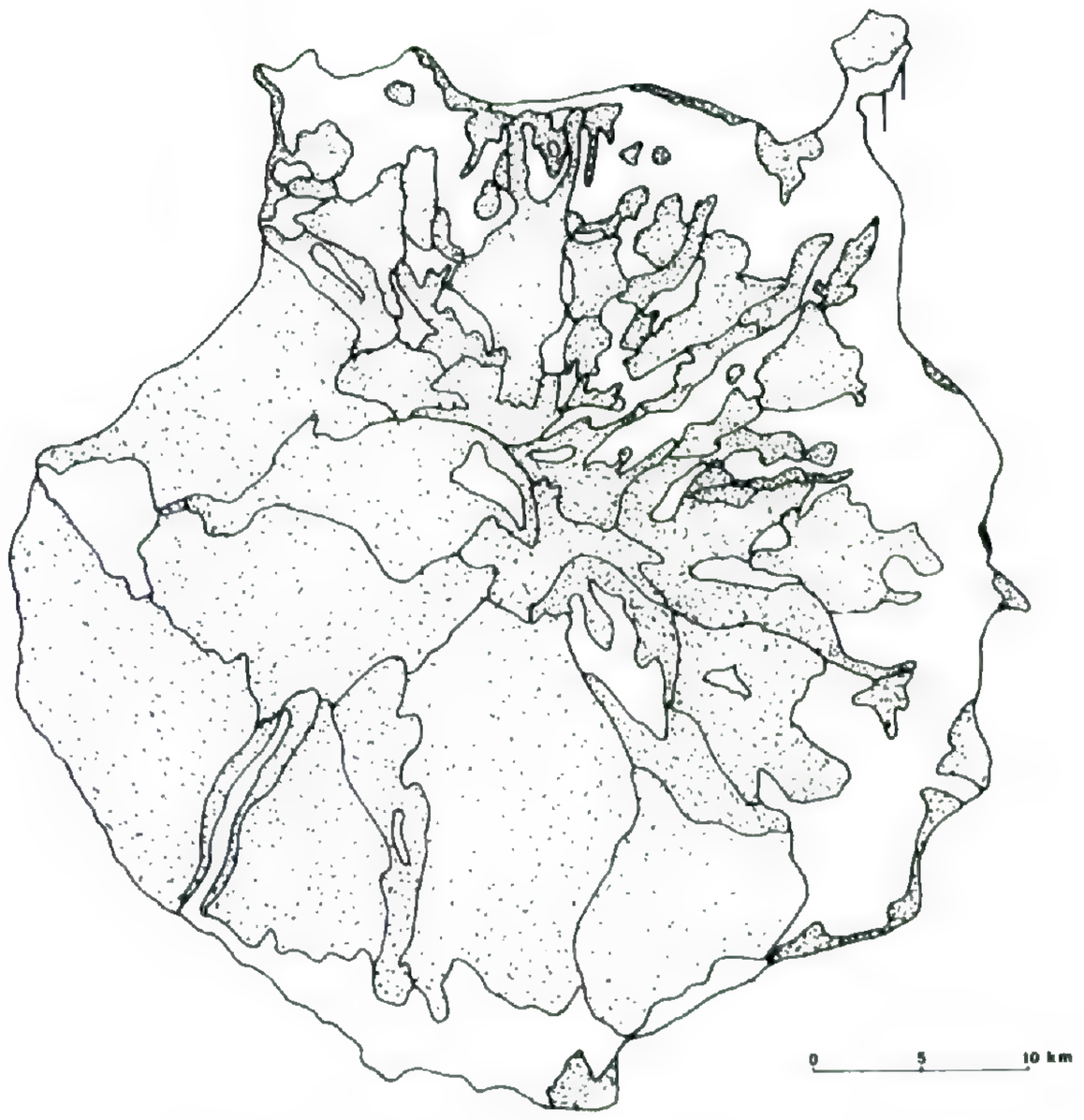

FIGURE 8. Areas proposed for protection in the Plan Especial de Protección de Espacios Naturales (PEPEN) by the Cabildo Insular de Gran Canaria.

on to the Canarian government for definitive approval following which the Directorate General for the Environment will have full responsibility for implementation of the legislation. It is, however, already being used as a guideline document by the Regional Planning Commission for authorization of planning permission. It was also used by the Canarian government's Environment Department as the basis for their 1987 Law on Protected Areas of Natural Interest, although in this case the total area was reduced as some of the areas given a lower level of protection in our plan did not fit into the scale of protection envisaged in the national law.

Conservation research

One of the most important conservation roles for a modern botanical garden involves conservation-oriented research. The fact that many gardens and their staffs have not yet come to grips with this new field does not diminish its importance, as the papers presented at the recent symposium on Botanic Gardens and World Conservation Strategy show (Bramwell et al., 1987). In the Canary Islands, the "Viera y Clavijo" garden was originally set up as a center for the study of the local endemic flora, and over the past few years our work has been mainly directed toward conservation problems and particularly the interface between in situ and ex situ conservation.

Research on individual species

At least 120 of the 500 or so endemic plants of the islands are critically endangered and are potential subjects for conservation-oriented research.

Initial studies have generally involved field observation, distribution mapping, population numbers and size, age structure, and other features leading to a comprehensive picture of the situation of each species in the field. This has been followed by more critical studies of habitat and ecology in many cases. For example, we tried initially to grow the very rare and highly endangered *Lotus kunkelii* in tissue culture, but failed until we carried out detailed studies of its natural substrate and found that the pH reached as high as 8.5 when temporary pools formed in the wet season dried out. We now have cultures of this species growing in a special high-pH medium.

Reproductive biology of many species has also been studied—for example, pollination in some of our extremely rare red- and orange-flowered plants, such as *Isoplexis*, *Lavatera*, *Scrophularia*, *Lotus*, and *Canarina*. Most of these, if they grew on the African mainland, would almost certainly be pollinated by sunbirds (Nectarinidae), but there are no sunbirds in the Canaries. Recent research has shown, however, that several mainly insectivorous birds not usually associated with pollination (*Phylloscopus* and *Sylvia* species) have taken over the role, and pollen samples collected at random from the heads of such birds have been positively identified as coming from such plants as *Isoplexis isabelliana* and *Canarina canariensis*. We have filmed pollination taking place in the natural habitat.

The spectrum of floral structure of bird-pollinated flowers in the Canaries is relatively narrow and does not include the long, narrow-tubed *Aloe* type. Observing the behavior of *Phylloscopus* species on cultivated *Aloe*, we found that it becomes a nectar-thief breaking into the base of the tube because its beak is too short to reach the nectar by normal means and, therefore, does not effectively pollinate long, narrow flowers. The surviving Canary bird-pollinated endemics all have relatively wide throats and short floral tubes.

Since the establishment five years ago of a seed bank for the long-term storage of endemic species, we have been involved in the study of seed production and biology of a considerable number of endangered species. In many cases, for example, *Tanacetum ptarmaciflorum*, where germination is naturally very low (9%), this can be considerably

improved (to over 60%), by treatment with gibberellic acid. We now have a large study program on germination and seedling establishment with a view to projects of restocking and reintroduction of species from the seed bank.

The seed bank provides material for a number of other research activities. When samples are removed from the bank for routine germination testing, any seedlings obtained can be used for studies that contribute to our knowledge of the species involved. Plants are grown for karyotype analysis and chromosome behavior, and study of variation, especially if the seed originates from very small, wild populations. Cotyledons, for example, can be used to establish tissue cultures, and seedlings are passed on to the garden nurseries for planting and use in educational displays and other purposes.

Recently conservationists have taken up the flag of biodiversity on a large scale, and in the Canaries this trend has been followed via the establishment of two projects under the name CODIGEN (Conservation of Genetic Diversity).

The first of these is a data-collecting project covering crop–plant relatives and known potential resource species in the Canarian flora. The project is being carried out in three phases.

1. An analysis of the actual situation of each species, distribution, biological cycle, potential and actual reproductive capacity, ecology, state of conservation, and classification according to the IUCN Red Data Book System.

2. Evaluation of each species as a potential resource and the genetic diversity it represents, closeness of relationship to the crop species, known disease resistance or tolerance, possible use in plant breeding, direct uses and scientific value.

3. Recommendations on conservation measures needed to protect each species, minimum number of populations, types of reserve, the need for ex situ conservation in gene banks or living collections, including possibilities for restocking in the natural habitat.

The final report is now available and has been handed over to the Canarian government for consideration in future conservation policy.

The second project is the creation of a conservation model for a single species of major value as a natural resource and for this we chose the Macaronesian endemic grass *Dactylis smithii*, which is a member of the *Dactylis glomerata* (cocksfoot) complex.

The aim of the project, which started in May 1988, is to review the distribution and morphological, ecological, and geographical variation within the species as a first phase and then attempt to study genetic diversity by means of karyology, protein and isozyme analysis, and then select natural variants for recommendation to plant breeders and evaluate the usefulness of this rare species as a forage grass via experimental cultivation. It could become an important species for dry-zone pastures. At the same time, the conservation situation of each natural population will be monitored and recommendations will be made for conservation.

Restoration of vegetation

A new field into which the botanical garden research staff members are also moving is what can broadly be termed restoration biology. This involves, at the simplest level, restocking individuals into an already existing population to increase numbers and variability in the natural population. This has been done successfully during a pilot project funded by WWF/SSC for *Senecio hadrosomus*; plants were grown in tissue culture from explants collected from a range of the surviving wild individuals, and the reintroduced individuals have been monitored over almost two years. Original reintroduction losses were high for this species but surviving individuals are thriving. There is again, however, a need for specialized research in this field if reintroduction is to become a viable means of conservation.

Our attempts to reestablish areas of Canarian laurel forest were successful in that young trees have been reintroduced in former forest areas. Our experience with this showed that in the forest ecosystem the development of the understory layer of shrubs, many of these important and rare endemics (e.g., *Sideritis discolor*, *Isoplexis chalcantha*), depends on the age structure and life cycle of the dominant trees, and the shrub species seem only to be able to establish themselves when gaps occur in the canopy. We need, therefore, to study the age structure of the dominant communities, species density, spatial organization, specialized niches, competition, effects of weeds and exotics, and a whole host of other factors in order to reconstitute ecosystems. Botanical gardens are probably among the most appropriate places for experimental work in this field.

Ecosystem reconstruction is an important subject for conservationists concerned with the floras of small islands, and there is an urgent need for research on restoration biology in island ecosystems.

Finally, I would like to mention micropropagation and in vitro cultivation of endangered species.

The techniques are now well known and are the subject of specialist literature, but their application to propagation of rare plants warrants some comment.

Cloning does not appear to be one of the most appropriate means of conserving genetic diversity, but under certain circumstances it can be a viable tool.

In our approach we have considered in vitro or micropropagation as useful in the following circumstances:

1. For species with chronically very small natural populations where the removal of seed or other propagating material may further damage natural capacity for reproduction and maintenance of diversity. There are in the Canaries several species known only from single localities and with populations of fewer than fifty individuals, for example, *Lotus kunkelii, Globularia ascanii, Helianthemum bystropogophyllum* (a very distinct species with a known population of less that 10 individuals), and we have successfully propagated several of these in vitro.

2. For species with low natural fertility, either because of genetic problems (pollen and seed viability) or susceptibility to natural predators of pollen or seed. For example, the Flor de Mayo Leñosa (*Senecio hadrosomus*) loses most of its naturally produced seed to larvae of the dipteran fly *Oedosphenella canariensis* (Suárez, 1982).

3. For propagation of species from remote areas when conventional propagating material, such as seed or cuttings, is not readily available.

4. For maintaining dioecious species in cultivation and enabling propagation when plants of only one sex are available. This situation is not infrequent in botanical gardens, and stock can be maintained and propagated for distribution to other gardens via in vitro cultivation.

5. As a means of maintaining germ plasm, especially of species with recalcitrant seeds, over long periods of time (Bramwell, in press).

6. For mass production of horticulturally valuable plants to relieve pressure on wild populations. An example of this is the very rare *Euphorbia handiensis* from the island of Fuerteventura, which is highly desirable for succulent collectors and has been overcollected in the field. We have the species in tissue culture and have propagated it in quantity, and we hope to make plants available to the succulent trade. We may also be able to restock as the natural habitat of the species is now included in the proposed reserves established under the new legislation mentioned previously.

Education

Environmental education is one of the most important aspects of our conservation activities, and we have a substantial program at the garden via organized garden visits and activities and through teacher-training courses, publicity, and extension activities. Two full-time teachers are seconded to the garden by the Education Department of the Canarian government and are responsible for daily visits, audio-visual shows, and a permanent exhibit on different aspects of the flora and fauna of the islands. (Currently there are two major themes, Canarian trees and birds of the Canary Islands.)

Teacher-training courses, particularly, are a very successful means of introducing awareness of environmental problems and conservation of local ecosystems and species into the local education system. Our work in this field was reviewed by Navarro (1987) in *Botanic Gardens and the World Conservation Strategy*.

Open days and public involvement with such projects as tree planting and the use of Canarian plants in local horticulture are also considered to be very productive in making the general public aware of the local flora and its value. From our nursery we supply plants to schools so that they can establish their own small Canarian gardens and to local councils for use in public parks and open spaces. During the next year we are planning to organize a tree planters club among school children to promote small-scale local planting of Canary palms (*Phoenix canariensis*), dragon trees (*Dracaena draco*), laurels (*Laurus azorica*), and other species.

Concluding Remarks

Conservation of biodiversity in the Canary Islands is a substantial subject for a single paper, and I have attempted to give a general picture of the situation and how the activities of one botanic garden fit into it at each level, from providing the scientific basis for legislation and planning to an extensive education program. Such activities require a dedicated team of workers, political and financial support, and the help of national and international conservation organizations. In order to coordinate this, we incorporated our conservation activities into a single project we called "Plantas y Futuro," which could be presented as a package to various funding bodies and for local support. The project covers mainly the field of research, including seed bank, micropropagation, a conservation data base, and the education program. It

was successful in obtaining funding at local (Cabildo Insular de Gran Canaria), regional (Gobierno de Canarias), national (Dirección General de Medio-Ambiente del Ministerio de Obras Publicas, Madrid), and international levels through the WWF/IUCN Plants Program, as well as from a local private foundation (Los Palmitos), who donated a microcomputer and a research fellowship for work on *Euphorbia handiensis*.

Much more still needs to be done before we can claim that the future of the Canarian flora and fauna is secured, but we seem to be moving in the right direction. Unfortunately this is still not enough, nor is it on a time-scale that will result in the conservation of many species and ecosystems. However, knowing this should stimulate an even greater effort in the future.

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INTEGRATED STRATEGIES FOR CONSERVING PLANT GENETIC DIVERSITY[1]

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ABSTRACT

As the intensity and magnitude of threats to biological diversity increase worldwide, conservation strategies must develop accordingly in three respects. First, conservation efforts must address all levels of biological organization, not simply species diversity; an overemphasis on species-level conservation risks missing biologically significant diversity at higher and lower levels of organization. Second, conservation measures must be conceived in response to particular threats or impacts to the biological entity of concern. Finally, the full spectrum of conservation resources must be employed in a coordinated manner without exclusive reliance on any single approach. By integrating information, needs, and resources in these three areas, a higher degree of protection is attainable for plant diversity than is possible by any single strategy. It is this inherently multidisciplinary approach that characterizes integrated conservation strategies.

Current threats to the survival of global plant diversity, and the biological and economic consequences of its decline, have been well-documented and publicized (Myers, 1979, 1987; Davis et al., 1986; Brown, 1987; Raven, 1987; Wilson, 1988). The threats appear as diverse as the plants themselves: habitats are fragmented, ranges reduced, and populations extirpated by virtually every known human use of land, from subsistence agriculture in the Third World tropics to resource extraction and recreation in developed nations.

Enormous investments are made each year in programs intended to conserve natural diversity in order to head off biological disaster. For instance, by 1985 the cumulative expenditures of the World Wildlife Fund, a private conservation organization, reached over $100 million on 4,000 projects in 130 countries (Phillips, 1986); The Nature Conservancy, IUCN, and many other conservation organizations maintain similarly extensive programs. Nonetheless, the pace of species decline and habitat destruction continues virtually unabated on a global scale, suggesting an unprecedented loss of biological diversity (Myers, 1979; Raven, 1987; Wilson, 1988). Despite persistent efforts by public and private conservation organizations, the pressures of population growth and demands on natural resources appear to be far greater than the ability to contain or redirect them.

Under such circumstances it is vitally important to set priorities clearly and to allocate scarce conservation resources carefully; no single method will suffice to provide adequate protection for biological diversity. Given the persistence and complexity of threats to biological systems, conservation cannot rely exclusively on any one approach, such as legal protection for species or acquisition of land, to accomplish its broadest aims (Given, 1987; Falk, 1987, 1989b; Jenkins, 1989). The increasing pace of destruction, continued shortage of resources for conservation, and the exigencies of resource development and population growth demand new models that draw on a wide range of tools and have the potential to build broad coalitions of support.

A trend toward more integrative, synthetic modes of conservation exists in the programs of such organizations as the International Union for Conservation of Nature and Natural Resources (IUCN, 1980; Bramwell et al., 1987), The Nature Conservancy (Morse, 1987; Jenkins, 1989), Conservation International (1988), World Wildlife Fund (Phillips, 1986), Center for Plant Conservation (Falk, 1987, 1989b; Falk & McMahan, 1988). These agencies increasingly emphasize reciprocal interactions of conservation and economic development, and collaborative, multi-agency projects. These efforts thus illustrate an emerging model of integrated conservation strategies that show considerable promise for protecting biological diversity in coming decades. This paper will explore several elements of an integrated conservation approach,

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examining as an example efforts to prevent rare plant extinction in the United States.

The Integrated Conservation Model

The integrated conservation model is based on the assessment and synthesis of three basic sets of information (Falk, 1989b). These include (i) determination of the biological entity of concern, including definition of the target level of biological organization; (ii) identification of the threats to this entity; and (iii) consideration of the full range of conservation resources that may be brought to bear on the problem. A salient characteristic of integrated conservation approaches, then, is that they deliberately seek a broad base of information about a conservation problem and employ a wide range of complementary tools to accomplish a given objective.

DEFINING A TARGET LEVEL OF BIOLOGICAL ORGANIZATION

The term "biodiversity" is often used in the general conservation literature without clear definition. Diversity means a range of variety or difference, and as such exists among alleles, individuals, populations, ecotypes, taxa, communities, and ecosystems. "Biological diversity" is frequently used as a shorthand reference to species diversity, but diversity at all levels of organization is of ecological and evolutionary consequence, and is therefore of concern to conservation (cf. MacMahon et al., 1978). Considerations of biological hierarchy influence both the feasibility of a particular conservation project and its cost-effectiveness. For example, a strategy well suited to capture genetic variation in a single plant population may be ineffective in protecting a whole ecosystem; conversely, acquiring and managing an entire ecosystem may be an expensive diversion of funds if all that is required in a specific instance is a sample of allelic variation at a particular locus. A later section of this paper will consider the conservation of infraspecific genetic variation in rare plant species as an example of the importance of this dimension.

Taxon-oriented legal mandates such as the U.S. Endangered Species Act can be applied to conservation at multiple levels of diversity, although the application is occasionally difficult (Sidle & Bowman, 1988). For plants, the Definitions of the Act identify species and subspecies as the target level of hierarchy [Endangered Species Act of 1973, as amended, 16 U.S.C. 1531 *et seq.*, Section 3(16)]. In some respects, programs such as those of The Nature Conservancy, which are designed to function at several levels of biological hierarchy simultaneously, may thus be preferable. An "element of diversity" in the Conservancy's system may be anything from a population to an ecosystem (Jenkins, 1988). The latter approach is hampered primarily by the lack of commonly accepted classification schemes for communities and other higher orders of biological organization, although progress is being made in this direction (S. Buttrick, pers. comm.).

In extreme cases, a number of species have been reduced to a single individual; McMahan (1989b) estimated that there are four such taxa in the continental United States and two in Hawaii. Conservation in these extreme cases, where each individual plant is significant, must follow a different strategy than would be applied to a population. In some cases cuttings have been propagated to increase the number of ramets, but it is not known if species can survive such a severe bottleneck (Barrett & Kohn, in press).

DEFINING SPECIFIC THREATS TO THE ENTITY OF CONCERN

Having specified a target level of biological organization, it is next necessary to determine the threat to that entity as precisely as possible. Although outright destruction or conversion of habitat is unquestionably the largest single cause of endangerment, many other factors—for example, invasion of exotic species or alteration of successional influences such as fire—contribute to the decline of populations, extinction of species, and disruption of communities. Other causes of endangerment include competition with invasive species, overgrazing by feral or commercial herbivores, suppression of fire and other disruptions of the natural successional process, loss of pollinators or symbionts, alteration of surface and groundwater hydrology, reduction of population size below minimum viable population level, and long-term climatic changes. Endangerment factors such as these may not respect property ownership boundaries or legal mandates. Thus, while legal protection for land and species is a necessary condition for conservation, specific threats to species and community diversity may require a long-term commitment to site management and stewardship (Jenkins, 1989). This approach assumes that the causality of threat is fully known; in fact, there is frequently only anecdotal information or casual observation of trends or causes of decline, especially for communities. Recovery plans developed by the United States Fish and Wildlife Services and Biological Manage-

ment Abstracts of The Nature Conservancy provide a growing data base on threats, but the accumulation of such information is slow in relation to the overall scale of endangerment. For instance, as of June 1989 there were 85 recovery plans completed for the 208 federally threatened and endangered plant species (U.S. Fish and Wildlife Service, 1989), out of a total of approximately 5,000 rare or threatened taxa in the United States.

Illegal collecting illustrates a cause of endangerment that may not be controlled simply by acquisition of land. For many U.S. plants, overcollecting and vandalism represent a serious component of endangerment; examples include *Pediocactus knowltonii* L. Benson, *Lilium occidentale* Purdy, *Lilium grayi* S. Wats., *Ancistrocactus tobuschii* (W. T. Marsh.) W. T. Marsh. ex Backeberg, and *Betula uber* (Ashe) Fern. (Center for Plant Conservation, 1987b; Olwell et al., 1987; Stafford, 1989).

Herbivore browsing represents a particularly intractable source of endangerment, especially grazing and seed predation by feral and domestic cattle, sheep, goats, deer, and rodents. In many instances, this is the primary cause of decline, including *Alectryon macrococcus* Radlk., *Phacelia argillacea* Atwood, *Agave arizonica* Gentry & J. H. Weber, *A. murpheyi* F. Gibson, *Pritchardia munroii* Rock, *Zizania texana* A. S. Hitchc., and *Hibiscadelphus distans* Bishop & Herbst (DeLamater & Hodgson, 1987; Center for Plant Conservation, 1988a, b).

THE CONSERVATION SPECTRUM

The use of a wide range of conservation methods is compelled largely by the diversity in objects of conservation and threats they encounter. The integrated conservation method is thus highly site-specific and situational, in contrast to traditional approaches that they have tended to greater uniformity by stressing legal protection or fee-simple land acquisition in every case (Falk, 1989a).

The early history of conservation in the United States was characterized by the setting aside of vast tracts of land—the Adirondacks Forest Preserve, Yellowstone and Yosemite national parks. The era of massive protection and acquisition on this scale in the United States probably concluded with passage of the Alaska National Interest Land Conservation Act in 1980; although some substantial areas remain unprotected, most acquisition is now on a smaller scale. For instance, in 1985–1987 the average land acquisition project of The Nature Conservancy was approximately 423 acres (The Nature Conservancy national office data). Moreover, the total land area protected by private conservation organizations (between 3.5 and 4.0 million acres) is dwarfed by other types of ownership such as Native American tribal lands, which include more than 25 million acres in the Southwest alone (Nabhan, 1988).

Furthermore, in the United States west of the Rocky Mountains, approximately 47% of the total land area is owned by the federal government, with another 21% owned by state and local governments (United States Geological Survey, 1970). Thus, in the United States, much of this land is managed by the Bureau of Land Management, United States Forest Service, and other agencies with multiple-use mandates that include resource extraction and recreation as well as conservation.

A further consideration from a strategic point of view is the extent of human disruption in the functioning of natural systems and the distribution of species. True wilderness—that is, a natural system unaffected by human activity—is declining steadily worldwide. In the continental United States it is restricted almost entirely to Alaska and parts of the Great Basin, and even in the rest of North America wilderness is found primarily in the boreal forests and tundra of northern Canada. Virtually all other land has been affected by human activity, however slightly, whether by outright destruction or conversion of habitat, or by removal of predators, pollinators, disruption of migratory pathways, introduction of exotic species, suppression of fire, or alteration of basic biogeochemical cycles and environmental parameters. Even fencing a habitat refuge may alter movement of animal species, and for wide-ranging species a protected area may encompass only a portion of their total range (see Janzen, 1989). These influences have precipitated a dramatic shift away from the "laissez-faire" ethic that dominated conservation philosophy earlier in this century (Hays, 1959; Sober, 1986) toward an acceptance of biological management, which may be defined as a calculated intervention into the functioning of a natural system in order to attain a stated biological construction or goal (see also Western & Pearl, 1989). As a consequence, the palette of conservation practice has expanded considerably in recent decades, and now includes botanic gardens, arboreta, and seed banks (Bramwell et al., 1987; Jenkins, 1989), as well as more extensive programs of park management (Hales, 1989) and restoration (Jordan et al., 1987). Each of these conservation methods is most effective at particular levels of biological hierarchy. For example, seed banks are well suited to conserve allelic diversity within a population, but inherently incapa-

ble of conserving communities or ecosystems. Nonetheless, they may play a key role in an overall integrated strategy to address diversity at multiple levels of organization.

In many respects these different approaches to conservation are distinguished more by degree than by kind. For instance, successional management of a fire-adapted ecosystem, such as prairie or savanna, may involve fencing, site preparation, controlled burns, and reseeding with native species. Such a management regime may be distinguished from a reintroduction program only by the number of years during which a particular species was absent from the site, or from ecological restoration only by the extent of reconstruction of a whole community. Modern land conservation management is essentially management of ecological succession, whether practiced as natural area stewardship, community restoration, or species reintroduction. Ironically, often the tools of destruction—bulldozer, herbicide, chainsaw, and fire—are, in different hands, the tools of conservation. The underlying continuity among these modes of conservation resolves the obsolete dichotomy between ex situ and in situ conservation; neither exists in a pure form. In place of polarized alternatives, integrated conservation substitutes a spectrum of compatible, mutually reinforcing methods.

Case Studies in Integrated Conservation

The integrated approach is being used with increasing frequency in the conservation of rare plant species in the United States (Falk, 1987, 1988; Falk & McMahan, 1988). The following examples illustrate its utility and the diversity of situations in which it may be applied. Other examples of integrated conservation of endangered plant species are given in Table 1.

Florida torreya (*Torreya taxifolia* Arn.) is endemic to cool microclimate refugia in the Apalachicola River basin of Florida and Georgia. The species occurs largely on protected land in Florida's Torreya State Park, the Apalachicola Bluffs and Ravines Preserve of The Nature Conservancy, and land owned by the U.S. Corps of Engineers and a city park department (U.S. Fish and Wildlife Service, 1986; McMahan, 1989a), but remains endangered by a severe fungal infection that prevents trees from reaching reproductive age. The primary conservation target is the population and species level, since the habitat is essentially protected. Conservation measures in a program being undertaken by the Center for Plant Conservation in cooperation with The Nature Conservancy and other agencies include isolation and identification of native and exotic fungal pathogens, determination of natural ecological factors, such as fire, that may inhibit fungal growth and reproduction, and placement of experimental populations in more northerly locations to determine optimal climate and potential range.

In many cases the causes of population and species decline are largely ecological. For example, Malheur wire-lettuce (*Stephanomeria malheurensis* Gottlieb) was extirpated from its only known locality in east-central Oregon by overgrazing, competition, and fire (Brauner, 1988). Recovery was targeted at the species and population level, with an effort to reestablish the species in its original habitat using proposals collected by Gottlieb and germinated at the Berry Botanic Garden in Portland, Oregon. The recovery project, which was funded by the United States Fish and Wildlife Service and the Bureau of Land Management, also included a study of community dynamics, by testing the success of *S. malheurensis* seedlings with five dominant ground covers (Center for Plant Conservation, 1987a; U.S. Fish and Wildlife Service, 1982).

An interesting case of conservation below the species level is Catalina Mountain mahogany (*Cercocarpus traskiae* Eastw.) endemic to a single canyon on Santa Catalina Island in California's Channel Islands, and perhaps the rarest tree on the continent (Rieseberg, 1988). The taxon has been drastically reduced by grazing and uprooting by feral and introduced goats, pigs, sheep, mule deer, and bison. Earlier impacts included heavy cutting by settlers in the last century for use in making fenceposts. Many of these impacts were eliminated or moderated by acquisition of the land and fencing of the *C. traskiae* population in the 1970s by the Santa Catalina Conservancy. This protection, however, revealed a more insidious threat to the species by hybridization with the more widespread *C. betuloides* Nutt. ex T. & G. var. *blanchae* (C. K. Schneid) Little, which overlaps *C. traskiae* in range. Electrophoretic and morphological analysis by Rieseberg et al. (1989b) determined that as many as five of the seven remaining adult trees were hybrids, as were several of the new seedlings within the fenced area, suggesting that swamping of the *C. traskiae* gene pool by *C. betuloides* var. *blanchae* is occurring. Recommendations for biological management included removing adjacent stands of *C. betuloides* var. *blanchae*, transplant of *C. traskiae*, to protected sites elsewhere on Santa Catalina Island, and removal of nonnative herbivores from the area.

TABLE 1. Recent studies of integrated conservation and management of rare U.S. plant taxa.

Taxa	References
Agave arizonica	DeLamater & Hodgson (1987)
Arctostaphylos pallida	Amme & Havlik (1987)
Arctostaphylos uva-ursi subsp. *leobreweri*	Reid & Walsh (1987)
Banara vanderbiltii	Popenoe (1988)
Cercocarpus traskiae	Rieseberg (1988); Rieseberg et al. (1989a)
Chrysopsis floridana	Wallace & McMahan (1988)
Erysimum menziesii	Ferreira & Smith (1987)
Goetzia elegans	Center for Plant Conservation (1988a)
Helianthus schweinitzii	South Carolina Wildlife & Marine Resources Dept. (1989)
Hemizonia arida	Faull (1987)
Hibiscus dasycalyx	McMahan (1988)
Iliamna corei	Thompson (1988a)
Monardella linodes subsp. *viminea*	Scheid (1987)
Pediocactus knowltonii	Milne (1987); Olwell et al. (1987); Stafford (1989)
Penstemon barrettiae	Schwartz (1988); Thompson (1988b); Kierstead (in press)
Spigelia gentianoides	Rogers (1988)
Stephanomeria malheurensis	U.S. Fish and Wildlife Service (1982); Center for Plant Conservation (1987a); Brauner (1988)
Styrax texana	Cox (1987)
Trifolium stoloniferum	Bartgis (1985); Pickering (1989)
Torreya taxifolia	U.S. Fish and Wildlife Service (1986); McMahan (1989a)
Warea amplexifolia	Center for Plant Conservation (1988a); Wallace & McMahan (1988)
Zizania texana	Center for Plant Conservation (1988a)

CONSERVATION OF INFRASPECIFIC GENETIC DIVERSITY IN RARE SPECIES

Effective conservation of biological diversity requires a sound basis in scientific understanding of the entities being protected; this may be viewed as a fundamental axiom of conservation biology (Lacy, 1987). Nowhere is this principle more important than for conservation efforts for rare and endangered plants, many of which are highly endemic or reduced in range and facing serious threats to their survival. Conservation and management of these species often have little margin for error, and likewise little opportunity for extensive field experimentation to determine optimal management techniques.

Biological management, moreover, is an information-intensive undertaking, requiring detailed information about the ecology, population biology, genetics, and representative biology of the target species. Such information, however, is in short supply in the literature; Table 2 lists recent published research on the population biology and genetics of rare U.S. plants. The paucity of information is in part due to the nature of the subject species themselves; endangered species are often restricted to one or two sites in remote areas, with poorly documented phenology and population history. Ironically, we often have the least biological information on the very species about which we need to know the most.

An understanding of patterns of genetic variation in rare plants is of particular importance for conservation strategies that involve offsite collection, maintenance, and reintroduction of living plant germplasm. The distribution of genetic variation within and among populations and factors that may influence that distribution are crucial to the establishment of genetically representative offsite collections. Similarly, inbreeding, drift, and methods of assessing genetic diversity within species are important considerations in long-term management of these collections for conservation and research (see Millar, 1987; Center for Plant Conservation, 1986; Kruckeberg & Rabinowitz, 1985).

A case in point is the conservation and management of genetic variation within rare species, which are frequently of the most critical conservation concern (see Huenneke & Holsinger, 1986; Lacy, 1988). Studies of genetic variation in rare plants are still infrequent in the literature. For example, a series of papers on the rare endemic *Pedicularis furbishiae* S. Wats. has contributed useful knowledge to its conservation (Macior, 1980; Menges et al., 1985; Gawler et al., 1987; Waller et al., 1987), but few rare taxa have been studied in such detail.

Several other recent studies of the genetics of

TABLE 2. Studies of the population biology, genetics, and ecology of rare North American plant taxa.

Taxa	References
Abies bracteata	Ledig (1987)
Aeschynomene virginica	Carulli & Fairbrothers (1988)
Astragalus osterhoutii and *A. linofolius*	Karron (1987a); Karron et al. (1988)
Astragalus tennesseensis	Bowles et al. (1987b)
Calochortus spp.	Fiedler (1986, 1987)
Cercocarpus traskiae	Rieseberg et al. (1989b); Rieseberg (in press)
Chrysosplenium iowense	Schwartz (1985)
Clarkia spp.	Gottlieb (1973, 1974)
Clematis fremontii	Erickson (1945); Learn & Schaal (1987)
Collomia rawsoniana	Taylor et al. (1987)
Cupressus macrocarpa	Conkle (1987)
Dedeckera eurekensis	Wiens et al. (1987, 1988)
Erysimum menziesii	Berg (1987)
Helianthus exilis A. Gray	Rieseberg et al. (1988); Rieseberg (in press)
Helianthus paradoxus Heiser	Rieseberg et al. (submitted 1989a); Rieseberg (in press)
Helianthus praecox subsp. *hirtus*	Rieseberg & Doyle (1989)
Howellia aquatilis	Lesica et al. (1988)
Hymenoxys acaulis var. *glabra*	DeMauro (1989)
Leavenworthia spp.	Solbrig (1972)
Lespedeza leptostachya	Smith (1987)
Mimulus guttatus	Ritland & Ganders (1987a, b)
Oenothera organensis	Levin et al. (1979)
Orcuttia spp.	Griggs & Jain (1973)
Pedicularis furbishiae	Macior (1980); Menges et al. (1985); Gawler et al. (1987); Waller et al. (1987)
Pinus radiata	Millar et al. (1988)
Pinus torreyana	Ledig & Conkle (1983)
Plantago cordata	Meagher et al. (1978); Primack (1980); Bowles et al. (1987a)
Polygonum pensylvanicum	Kubetin & Schaal (1979)
Silene invisa	Taylor & Palmer (1987)
Warea amplexifolia	Wallace & McMahan (1988)

rare species have contributed valuable insight into the biology of these organisms, including the studies listed in Table 2. Nonetheless, considering that there are upward of 5,000 plant taxa of conservation concern in the United States alone—representing close to 20% of the entire national flora—the overall extent of research into the population biology and genetics of rare species is disappointingly small.

One illustration of the need for population biological data for conservation is the clasping warea (*Warea amplexifolia* (Nutt.)), endemic to central peninsular Florida. The two remaining populations are composed of fewer than 100 individuals each; as the species is annual, population sizes fluctuate dramatically from year to year (Center for Plant Conservation, 1988a; Wallace & McMahan, 1988). In addition to the dangers of demographic stochasticity, seed set has been extremely low in recent years, suggesting that the populations may be below a minimum viable population threshold and hence subjected to intensified levels of inbreeding.

Karron (1987a; Karron et al., 1988) compared levels of genetic polymorphism in common and widespread taxa within a genus (*Astragalus*, Fabaceae) and observed that while some rare species are genetically depauperate, others exhibit as much polymorphism as more widespread congeners (see also Karron, 1987b). Other studies of genetic variation in rare species such as those of *Pinus radiata* (Millar et al., 1988) indicate unexpectedly high levels of polymorphism even among severely restricted taxa (see also Ledig & Conkle, 1983; Conkle, 1987; Ledig, 1987). Thus, while some species conform to Hamrick's findings (1983; Hamrick et al., 1979, 1981) that endemic species generally exhibit lower diversity than widespread species, many other species do not. Historical, reproductive, and ecological factors may account for much of the observed variation in rare species, but the number of comparative studies in general is still small.

The ecological and evolutionary significance of genetic variability in rare species is still a matter of significant debate. Huenneke (in press), for in-

stance, argues that the loss of even low-frequency alleles in species that are already genetically reduced may result in significantly lower evolutionary fitness. By contrast, there is some evidence that plants may be able to survive and re-radiate following severe genetic bottleneck events (Templeton & Reid, 1983; Barrett & Kohn, in press; see also Barton & Charlesworth, 1984). Many species are susceptible to inbreeding at low effective population numbers, but Menges (in press) has discussed a variety of reproductive strategies and other life history characteristics that may tend to buffer plants from the effect of low population size.

The consequences for conservation of an inadequate base of population genetic research should not be underestimated. For instance, land acquisition programs for habitat conservation or field sampling for offsite germplasm collections are often undertaken to help ensure the survival of rare species and to prevent anthropogenic extinctions. But without an understanding of the partitioning of genetic variation in populations of rare species, or in the ecological and evolutionary impact of inbreeding in small populations, there may be insufficient criteria to guide the scientific selection, design, and management of reserves or offsite germplasm sampling or reintroduction programs. In any event, since rare species often occur in small, isolated populations characterized by intense inbreeding at low effective population sizes, conservation of intraspecific genetic diversity must be recognized as critically important in the management of these taxa.

Conclusion

Rare plant species present a particularly acute set of problems in the conservation of biological diversity. Because of their restricted geographic ranges, frequently narrow ecological amplitudes, and vulnerabilities to drift, inbreeding, and stochastic events, endangered species represent critical priorities in biodiversity conservation. There is a pressing need for improved knowledge of their biology, especially in the areas of population biology, genetics, and ecology.

In many cases, an integrated conservation approach offers the only realistic hope of preventing extinction. By focusing on a defined level of biological hierarchy, integrated strategies help clarify the objects of conservation. By articulating the threats specific to that entity, such strategies identify the proximate causes of decline; this enables the use of the widest range of conservation methods from the spectrum of available resources. And, by integrating these basic elements into an action plan that utilizes a wide variety of conservation resources, plant biodiversity—from the allele to the community—may be best protected.

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CONSERVING BOTANICAL DIVERSITY ON A GLOBAL SCALE[1]

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ABSTRACT

As the world moves toward the twenty-first century, it seems ill prepared to cope with increasing social, economic, and demographic problems. It is not surprising that loss of biodiversity is not perceived as a problem by many people. Current depletion rates are reaching serious proportions. Attention is particularly focused on losses to moist tropical forests and the need to monitor this at a variety of levels: area and quality of habitat, species extinction, and loss of genetic variability. However, conservation of tropical forest must not be at the expense of other habitats and ecosystems. Alarming losses are occurring in many other systems, such as wetlands and Mediterranean shrublands. The plants of even such recently pristine regions as the Antarctic are under pressure from human influences. Future scenarios are not easy to construct as there are many uncertainties. Major deleterious factors could be: global climatic changes, especially through the greenhouse effect and alteration in the ozone layer around the earth; soil depletion, genetic loss, and climatic changes resulting from tropical forest loss; increase in the human population; economic instability and imbalances in distribution of wealth; and decreased resources for research and biological conservation. In view of this, there is need to question whether conventional strategies chiefly involving protected natural areas, botanic gardens, and gene banks can cope with future needs. Focal points for short-term and long-term action are suggested. There is need to understand with greater precision the processes of extinction and to elaborate and test extinction models. Management of modified landscapes is likely to achieve greater prominence in the future but needs to be based on sound biological theory. Conservation managers and biologists will need to be innovative and bold, perhaps making decisions that may be unpopular with some supporters of conservation but may be necessary for the long-term well-being of the biosphere. An increased level of cooperation is necessary; currently this is hampered in some countries by a "free market" philosophy of competitive funding. Adequate resources for conservation are essential, and this means establishing a better case for research and management funding, clearer definition of objectives, and greater accountability by scientists. Perhaps, above all, a new ethic is long overdue, marked by a return to the concept of global and regional commons with recognition of interdependence rather than independence. There is danger in the view that "everyone is a conservationist at heart" unless there is clear understanding of what this means in practical terms to each individual. Perhaps the greatest danger facing conservation is loss of biodiversity by slow attrition. Awareness of the value and wonder of diversity is probably the best safeguard against this, which means that conservation research and management must not only be directed for the good of plants and animals, but must be communicated to people living alongside them.

> If we sell you our land, love it as we've loved it. Care for it as we've cared for it. Hold in your mind the memory of the land as it is when you take it . . . and with all your strength, with all your mind, with all your heart, preserve it for your children—Chief Seattle, 1854.

Recently, I telephoned the head of science at a local high school. During the conversation I asked why there is so little conservation in the senior science syllabus. He thought and answered, "Well, conservation of plants and animals was an issue in the 1970s, but it isn't really an issue now!" One of the questions that we need to address is exactly this: Is biological conservation an important issue today? If the answer is negative, then we are probably wasting our time being here today! Norman Myers (1979, p. 3) succinctly expressed the view of many people:

> Ask a man in the street what he thinks of the problem of disappearing species, and he may well reply that it would be a pity if the tiger or the blue whale disappeared. But he may well add that it would be no big deal, not as compared with crises of energy, population, food and pollution—the 'real' problems. In other words, he cares about disappearing species, but he cares about many other issues more: he simply

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does not see it as a critical issue. If the tiger were to go extinct tonight, the sun would still come up tomorrow morning.

Myers pointed out that his man in the street is quite correct in one respect—by tomorrow morning there is likely to be at least one fewer species on planet Earth than there was this morning.

Diversity is often expressed as numbers of taxa, and commonly we speak of conserving "species." But diversity can be expressed in many other ways such as morphology, size, color, function, range of habitats, and use by people. It is useful to distinguish three principal levels of diversity. Ecological diversity is expressed as diversity of habitats and ecosystems, the diversity we see in a mosaic of forest, grassland, wetland, and other habitat types throughout a landscape. Species diversity is expressed as numbers of taxa, reaching maximum levels in regions with high numbers of locally endemic species. Genetic diversity occurs at the level of genes, the building blocks of life which make one individual and population different from another.

Whatever the measure of diversity, there is little doubt that the world of plants is immensely varied. There are about 235,000 flowering and 270,000 nonflowering extant plant species (Raven et al., 1986; H. Synge, pers. comm., 1988; D. L. Hawkesworth, pers. comm., 1988). They occur in many different habitats from the tropics to polar regions, and from 100 m under the sea to over 6,000 m altitude. An exciting outcome of polar botany in recent years has been the discovery of plants in the Antarctic growing under environmental extremes formerly considered uninhabitable. This includes mosses growing on fumerolic soils of active volcanoes (Broady et al., 1987) and endolithic algae of the dry valleys of southern Victoria Land (Friedmann, 1982). The latter plants live in the interstices just below the surface of coarse-grained rock, demonstrating the persistence of life under the most adverse of environments. Plant diversity is essential to the Earth's biosphere as we know it. With the exception of some sulphur bacteria, all animals are ultimately dependent on the Earth's green mantle of photosynthetic plants.

What Are the Losses?

All species have a limited life in geological terms, whether it be measured in hundreds of thousands or tens of millions of years. But this is poor justification for the frequently offered counter to conservation that: "Because extinctions have always been occurring there is surely nothing to be concerned about. Does it matter if a few more species disappear?" This argument ignores the balance between extinction of some taxa and the evolution of others. What causes concern is that current rates of extinction are many times the natural background rate.

The present accelerating loss of species has been likened to mass extinctions of the geological past, where five particularly prominent "megaspasms" of extinction have been identified from the fossil record (Jablonski, 1986). Present extinction rates are at least several hundred times the current natural background rate, and it is argued that they will rise several orders of magnitude by early next century to constitute the greatest mass extinction for at least 65 million years (Myers, 1979; Ehrlich & Ehrlich, 1981; Jablonski, 1986). A unique feature of the present mass extinction is that it is primarily due to the impact of a single species, *Homo sapiens*.

Extinction rates are surprisingly hard to measure, especially on a global scale. What can now be measured reasonably accurately is the rate of loss of habitat. Remote sensing backed by ground surveys provides the key to this. The Global Environment Monitoring System (GEMS) and especially the Global Resources Information data base permit measurement on a continuing basis of habitat loss.

The emerging picture is disturbing. Taking evergreen, moist tropical forests as an example, there were probably about 1.6 billion hectares worldwide before widescale human-caused deforestation began to accelerate. Current deforestation rates have been conservatively estimated at about 30 hectares each minute or 15 million hectares annually; other estimates range up to over 26 million hectares each year (Roche & Dourojeanni, 1984; Myers, 1984a; Gradwohl & Greenberg, 1988). Of this, about 4.5 million hectares are disrupted by commercial logging, 2.5 million hectares by nonsustainable gathering of fuelwood, and at least 2 million hectares as a result of cattle ranching. But one of the principal forms of deforestation is the wave of slash and burn agriculture following opening up of forests by roads. Loss of forest due to small-scale cultivation involves perhaps as many as 250–300 million people occupying about 22% of present-day moist tropical forests (Myers, 1986a; Gradwohl & Greenberg, 1988). There has already been a loss of 27–37% of these forests, and a further 12–25% is likely to be lost before the end of this century (Simberloff, 1986).

However, not just loss of area is important, but also loss of quality. What to the layperson is intact forest may be botanically depauperate. Moist tropical forests, along with Mediterranean-type eco-

systems, are noted for their high level of biodiversity and for complex networks of interacting animals and plants.

Modern technology permits habitat conversion and timber extraction at rates undreamed of in the past. The tropical lumber industry has been likened to mining with extraction rates in most cases well in excess of sustainable yields (Whitmore, 1980).

For some smaller areas, such as the Brazilian state of Rondônia, quite precise data are available (Myers, 1986a; Prance, 1986, 1987). Rondônia has an area of 243,000 square kilometers, and before 1975, 1,200 square kilometers had been cleared of forest. At that stage, the population averaged about two people per square kilometer. By the late 1970s the population was increasing by almost 16% each year. Between the end of the 1970s and 1985 it doubled to over one million, an increase of over 1,000% since 1968. As the population increased so did deforestation, with more than 10,000 square kilometers cleared by 1980 and 17,000 square kilometers by 1985. Today there is a vast network of roads and farms throughout the forest, and removal of forest continues. The tragedy is that the rich soils that attracted farmers to Rondônia also made it home to a rich assemblage of indigenous animals and plants, many endemic to the region.

As the forests disappear, so do their component species. Worldwide, an alarming number of species are down to only a few individuals. An extreme example is the St. Helena olive (*Nesiota elliptica*), which is a monotypic genus and is only known from a single plant. Despite moderately successful initiatives to save the St. Helena flora, the St. Helena olive is still critically endangered (Cronk, 1987). Seed rarely sets and cuttings seem nearly impossible to strike. The remaining tree is old and vulnerable.

Similar examples come from the Pacific lowland of Ecuador, regarded by Myers (1988b) as one of the three most critical tropical forest "hot spots" where biodiversity is under threat. Since 1960 the original rainforest has been almost totally eliminated and converted to cash crops. A small remnant at Río Palenque of less than one square kilometer is now the only remaining site for 43 plant species, of which a good number, including *Dicliptera dodsonii* (an attractive vine known only from one plant) and the useful timber tree *Persea theobromifolia*, are known from very few individuals (Gentry, 1977; Lucas & Synge, 1978; Myers, 1988b). The adjacent Centinella Ridge once supported 100 endemic plant species which were eliminated by clearance for agriculture between 1980 and 1984 (Gentry, 1986; Myers, 1988b).

Loss of species, especially those with human appeal, sometimes attracts publicity, but loss of genetic variability within species is harder for the layperson to appreciate. Yet, in terms of usefulness to mankind and potential for evolution, loss of variability within some species may be just as significant as loss of some taxa. Loss of variability in wild populations of the Himalayan *Dioscorea deltoidea*, an important source of cortico-steroids, has direct commercial implications. Analyses of past collections indicated up to 6% of the steroid diosgenin, but recent analyses following intensive harvesting of wild populations have failed to reveal plants with more than 1% of this chemical (Gupta & Sethi, 1983).

Genetic erosion, which is "the loss of genes from a gene pool due to the elimination of populations because of such factors as the adoption of modern varieties and land clearing" (Plucknett et al., 1987), is an increasing problem. As farmers have adopted modern crop varieties and agricultural practices, they have tended to shift to monoculture and genetic simplification of farmlands. The genetic base of crops entering world trade has narrowed because of this. Simultaneously, there has been genetic erosion of wild genetic resources and landscapes through reduction in habitat quality and quantity, and extirpation of many populations containing distinct genotypes.

The significance of genetic erosion is demonstrated by the battle against grassy stunt virus in rice. This proved a serious pest of rice throughout much of South and Southeast Asia between the 1960s and late 1970s. The International Rice Research Institute (IRRI) tested thousands of breeding lines and wild species samples for resistance. Only a single sample, collected from a population of Indian *Oryza nivara* in 1963, showed resistance, and even this was restricted to three plants out of the sample of 30. From these three plants came the virus-resistant gene which was bred into cultivar IR36 and is now found in every high-yielding cultivar of rice grown in tropical Asia (Hoyt, 1988; Plucknett et al., 1987).

Losses are not confined to tropical forests. Alarming depletion rates are encountered in many ecosystems around the world. One-third of the planet's land area is semiarid or arid. In the arid tropics, desertification is a major problem, chiefly through unsustainable levels of agriculture, excessive removal of woody plants for fuel, faulty irrigation, and poor range management. Each year about 12 million hectares of this land deteriorates to agricultural worthlessness (Myers, 1984b). Mediterranean-type vegetation of some arid and semiarid regions is often highly diverse, sometimes with

many extremely local endemic species. However, as despised so-called nonproductive "scrub," it is frequently at risk through clearance for farmland and housing. The highly distinctive Mediterranean-type shrublands of the South African Cape are among the most diverse plant communities known, yet over 1,300 of their component species are under threat (Hall & Veldhuis, 1985), and perhaps as many as 350 plant extinctions may occur in the next 30–50 years unless major action is taken to rescue species (A. V. Hall, pers. comm. 1988).

Wetlands are particularly at risk, and increasing numbers of wetland species are found in lists of threatened species. Particularly alarming is pollution by new ultratoxic compounds formed through the dumping and subsequent mixing of substances such as chlorine and thiocyanates (Kaul, 1983). A complication in the management of wetlands is that they are often subject to natural periodic fluctuations in water level. These can be extremely difficult to replicate, especially when wildfowl shooters, fishermen, boat-owners, and other users demand different water levels to suit their particular requirements (Keddy & Reznicek, 1986; Spence, 1982). Edward Maltby (1986) pointed out that with the extirpation of wetland species we lose many opportunities to study such processes as anaerobic metabolism, salt tolerance, and natural detoxification.

Even in apparently pristine regions there is loss of habitat along with local extirpation of plants. The Antarctic is often cited as the last untouched wilderness, but even here, where less than 1% of the continent is ice-free, plants compete with Antarctic bases and camps for suitable habitat along the coast (Given, 1987). This raises many questions regarding the adequacy of environmental assessment and protection procedures in such regions, as well as the need for more stringently managed protected areas.

It is not enough to shut people out of a protected area. David Ehrenfeld (1986a) pointed out that you may be able to keep people out but you cannot fence out their introduced plants, acid rain, ozone, insecticide residues, drifting herbicide, heavy metals, and atmospheric particulates. He gave the example of Huchison Forest at Rutgers University, where entry is limited and the site is used only for "unobtrusive" ecological research. Yet the forest is increasingly invaded by alien animals and plants.

Present Efforts and Future Focal Points

An impressive effort is being made at present to conserve plant diversity worldwide. In the 1960s this started to gain momentum, leading to inventories, Red Data Books, population monitoring for conservation purposes, and setting aside reserves primarily for conservation of plant taxa and gene pools.

The most widespread and perhaps the most cost-effective means of conserving plants is by preservation of natural habitats. Many thousands of protected areas play a valuable role in preserving plants. They range from large national parks to small intensively managed nature reserves and remnant strips along roads and railways.

Some reserves require precise and constant management. In the fens of Cambridgeshire in England maintenance of specific water levels is critical to the survival of vegetation and rare species. In an increasing number of instances, depleted populations of plants are being reinforced by replanting programs, or there is deliberate habitat rehabilitation. However, this is usually costly and time consuming; too often management is minimal and best described as benign neglect. Too many protected areas exist only on paper. They have not been surveyed, gazetted, fenced, or properly identified on the ground, or their management is such that the features for which they were set up are no longer protected.

A second major approach to conservation is through botanic gardens or arboreta. There are probably about 1,500 botanic gardens worldwide, but their geographic distribution is far from satisfactory. About half are in temperate Europe. Of the remainder, only 30 are in tropical Africa, about 60 in South America, and just over 120 in tropical Asia—all areas of high biodiversity. Many gardens maintain large, botanically valuable collections and some have a long history of involvement in conservation. Some of the earlier tropical gardens were established as acclimatization gardens. The botanic garden at Bogor in Indonesia is the repository for large collections of species from Southeast Asia, including many of economic importance. Some gardens concentrate exclusively on indigenous species; examples are the National Botanic Gardens in Canberra, Australia and Kirstenbosch near Cape Town, South Africa. Both of these gardens have laboratories to carry out conservation research on rare species, involving study of propagation and reproductive biology, ethnobotany, and habitat requirements.

The 1980s have seen interest generated in setting up botanic garden networks; for instance, the Center for Plant Conservation with a network spanning North America. The National Collections Centre based at Wisley in England has identified several hundred collections of national significance

in the United Kingdom. Following initiatives at the Las Palmas botanic gardens conference in 1985, 1987 saw the launching of the Botanic Gardens Conservation Secretariat, which now incorporates over 140 gardens in 26 countries.

Systematic storage of seed and other propagating material in gene banks plays a vital role in conservation of crops and their wild relatives (Plucknett et al., 1987). Thirteen agricultural research centers are coordinated through the Consultative Group on International Agricultural Research, including the network coordinated by the International Board for Plant Genetic Resources (IBPGR) and centers such as the Rice Research Institute. There are many problems associated with long-term storage of wild species. Some species have very short-lived seeds, while in others seeds are recalcitrant or require specific germination procedures, which are difficult to simulate. Small numbers of available propagules can cause problems for gene banks used to dealing in hundreds of seeds or tubers in each sample. Some conservationists have concluded that seedbanks are expensive and vulnerable, and inadequate to preserve more than a fraction of even the recorded varieties of crop plants (Ehrenfeld, 1986a). Nevertheless, despite some shortcomings, gene bank storage should be attempted as an integral part of any long-term endangered species program. By the year 2000 over 90% of remaining variations of major crops should have been collected, stored, and evaluated, and many close wild relatives of crops will have been collected. By then the role of cryopreservation will have been assessed, and collecting and handling techniques for vegetative germ plasm will have been markedly improved (Plucknett et al., 1987).

Conservation is moving away rapidly from total reliance on traditional techniques to utilize new technology. In western Australia satellite data were used to locate habitat of the rarely seen subterranean orchid *Rhizanthella gardneri*—the data showed the orchid to be associated with a specific host and more widespread than formerly thought (Dixon & Pate, 1984). Electrophoresis and, less often, DNA analysis are being used to assess population variation and to elucidate probable breeding systems. Isozyme analysis of Californian conifers and Australian narrow-range endemics, e.g., *Eucalyptus caesia*, is indicating considerable genetic differences between species that otherwise appear similar and assists in estimating minimum viable population sizes. Tissue culture is being used for some orchids and other plants that are difficult to propagate by conventional means. Callus tissue can also serve to propagate plants in large numbers at predetermined times of the year for reestablishment in the wild.

Legislation and education are vital aspects of threatened species programs. In the international arena, the Convention on International Trade in Endangered Species of Fauna and Flora (CITES) plays a major regulatory role. Many countries have enacted legislation to protect rare and endangered species and their habitats, although often this is applicable only to the plants found on state-owned lands or to taking of plants for commercial purposes. Legislation and regulation are starting to give greater acknowledgment to traditional uses of and attitudes toward plants; this also involves recognition of traditional forms of resource ownership such as common property regimes.

A vital role of botanic gardens in particular must be to create an awareness of the need for plants and their conservation. The proportion of urban people in most countries is steadily rising; in 1980 half the world was urbanized, but by the year 2000 75% of people will live in cities. For these people botanic gardens provide a window into nature. For protected areas, too, education and awareness are important components of management. Study of a rural community's attitudes to a nearby conservation area in Natal showed that positive attitudes were generally correlated with greater affluence and education, and particularly with direct expe-rience of the benefits of the conservation area (Infield, 1988). This suggests that it is important to involve local people in conservation programs. A remarkable example of this is found at Guanacaste, Costa Rica, where Dan Janzen is involving local people in management, "hands-on" education, and interpretation. Janzen's philosophy is that the remnant forests of Guanacaste are a library, an archive, and a classroom for the indigenous people, as well as serving valuable scientific and conservation functions (Janzen, 1986).

The 1980s have seen increasing stress on demonstrating the value of biodiversity and the usefulness of plants to people. To some extent this has been a process of rediscovery by the developed nations of what was well known to many traditional societies in less-developed parts of the world. Ethnobotany has acquired a new respectability by demonstrating the degree to which wild plants are used (e.g., Myers, 1984a; Hanks, 1984; Plotkin, 1986; Prance et al., 1987). Quantitative studies of the use of trees by four tribes in Amazonia show that these rainforests contain an exceptionally large number of useful trees; up to 76% of tree species on inventory sites can be "useful" (Prance et al., 1987). About 75% of the medical needs of the

Third World are met by traditional herbal remedies (Adesiwojo et al., 1984). Scores of locally cultivated crop plants have potential to supplement the 20 plants that contribute 90% of the world's food. These include more than 20 root crops, legumes, grains, and fruits found in South America, which are "lost crops of the Incas" (Vietmeyer, 1986). There are conflicts: should ethnobotany stress "discovery" and commercialization of plants for worldwide use, or should it encourage a retention of traditional use; and should the emphasis be on conservation of plants and their habitats because they are "useful" to mankind?

Documentation, inventory, and monitoring are vital to all conservation strategies. It is essential to know not only what taxa are at risk, but the trends and priorities, and whether strategies are successful. At the global level key roles are played by organizations such as IUCN's monitoring center at Kew, the specialist groups of the IUCN Species Survival Commission, The Nature Conservancy, Conservation International, and WWF. Their role is crucial. But they cannot do all the work. There is urgent need to enhance existing national and regional data bases and to establish new ones.

Inventories are showing that in many countries 10–15% of the vascular flora is likely to be at risk. Unfortunately, only sketchy data are usually available for cryptogams, and there is urgent need to assess the risk for these. There is also an urgent need to develop a monitoring system at the population level that is useful to the local manager of a protected area and can contribute to global estimates of depletion. The Plantwatch concept—as it has been christened by IUCN—must be simple and quick to operate while asking the relevant questions. An important project is the identification and assessment of centers of plant diversity, some of which are global "hot spots" under a high degree of threat (Myers, 1986b, 1988b). In just three of the "hot spots" for tropical forests (Madagascar, the Atlantic coast of Brazil, and western Ecuador), Myers (1988b) estimated that some 6,200 plant and 124,000 animal species could become extinct. A pilot scheme developed by IUCN at Kew has identified almost 160 centers of plant diversity around the world. Greatest numbers are in tropical South America, Asia, and Africa, including oceanic islands such as Rapa, Mauritius, St. Helena, and the Chatham Islands (IUCN, 1987). These are key sites to monitor the state of biodiversity and must be priorities for recovery projects.

Despite past and present achievements, there must be some doubt as to whether they will stem the tide of biodiversity loss. As we move toward the twenty-first century, several focal points emerge. These are the need for a more biological approach with greater understanding of persistence and extinction processes, development of management strategies appropriate to human-disturbed ecosystems, adequate resources for conservation, greater innovation and boldness, and development of a renewed conservation ethic.

Understanding Persistence and Extinction

Prevention of extinction and maximizing persistence are major complementary aims of conservation. Yet we are far from a full understanding of either persistence or the precise mechanisms of extinction and their relationship to such factors as viable population size. A major change of perspective has been the adoption of a systems approach in the early 1980s distinguishing deterministic extinction from chance or stochastic extinction. It shows that four separate forces make key contributions to population extinction (Schaeffer, 1981). These are: demographic stochasticity (variation in population size leading to unacceptably low numbers), genetic stochasticity (excessive inbreeding and loss of selective variation), environmental stochasticity (environmental shocks received by all members of a population), and catastrophes.

This work has been extended by Gilpin & Soulé and incorporated into a conceptual model that recognizes three components (Gilpin & Soulé, 1986): "population phenotype," "environment," and "population structure and fitness." Environmental changes set up feedback loops of biological and environmental interactions that impact the population negatively. Gilpin & Soulé referred to these event trains as "extinction vortices" that can lead to extinction. They identified four distinct vortices triggered by various combinations of chance decrease in population size, decrease in genetic effective population size, decrease in population growth rate, and increase in the variance of population growth rate. The vortices can operate over different time scales and can interact in different combinations.

An important advance has been to distinguish deterministic extinction (when something essential is removed, such as habitat or food, or when something lethal is introduced, such as predation) from stochastic extinction resulting from random changes or environmental perturbation.

The Gilpin & Soulé model has several practical implications. It identifies demographic stochasticity as often being the immediate precursor to extinc-

tion, justifying concern for the future of small populations. It also indicates that two important factors in long-term persistence are the maintenance of relatively large areas of habitat and sufficiently large populations to ensure that random effects do not result in loss.

Genetic aspects of extinction and especially the effects of loss in heterozygosity are often emphasized. Concentration on loss in genetic variability alone may overlook other stochastic factors or the possibility of loss through catastrophe. Especially in highly dynamic ecosystems, such extirpation may result from other effects long before loss of fitness is significant.

Well-documented case studies of extinction in regions of high risk are urgently needed. One ongoing project that should provide some insights is the Minimum Critical Size of Ecosystems Project in Amazonia sponsored by WWF(US) and Brazil's National Institute for Amazon Research (Lovejoy et al., 1986). This is a long-term attempt to determine the effects of fragmentation on habitat and species. It takes advantage of the decree that when land is cleared for farming, 50% must be left as standing jungle. At the project site the pattern of clearance is designed to leave remnants of varying size from one hectare up to 10,000 hectares.

Results of the effects of size and area are starting to emerge; for instance, the decline of some animal populations in remnants up to 10 ha (Lovejoy et al., 1986). As one species is lost, populations of other species may also decline. The smallest Amazonian reserves are not large enough to support populations of army ants. As they disappear, so do birds dependent on the ants for food. The loss of these birds is likely to lead to loss of interacting species that are dispersal agents or pollinators for plants. Loss of the ants also affects decomposition of plant matter and the recycling of nutrients.

It is not sufficient to assume that once a population has reached a predetermined "safe" size it will survive for the forseeable future. Persistence is concerned with the probability that under certain conditions and with a population of particular size, there is X probability of existence for Y number of years. But the selection of persistence times has an ethical aspect. Some people might be content with a low probability of persistence for 100 years whereas others might demand a very high probability for 1,000 years.

An important aspect of extinction theory is that processes for plants may not be quite the same as those for at least some animals. Examination of palaeobotanical data and comparison with data on animal fossils shows that, although there are comparable bimodal extinction rates, major changes in the composition of vascular plant floras have not coincided with similar events in the animal kingdom (Knoll, 1986). Knoll suggested that in many instances plant extinctions appear to be related to competition with newly evolved taxa or to climatic change rather than other extrinsic events that have been suggested as causative factors in some animal extinctions.

Above all, a more rigorous biological approach to conservation is needed. Even such elementary data as broad classes of breeding system, pollination and dispersal vectors, and germination requirements are generally unknown for threatened plants. This seriously hinders development of effective management programs for plant species. There is a severe shortage of experienced ecologists who can make management decisions for large areas of rainforest, wetlands, and shrublands. There seem to be no lack of students who want to be ecologists (or taxonomists and reproductive biologists), but as Les Kaufman vividly expressed the problem (Kaufman, 1986): "Ecologists somehow never quite 'made it' alongside those professionals whose services are viewed as essential to society. . . . But what about a messed-up ecosystem? We have yet to produce a school of competent ecological engineers."

Managing in Modified Habitats

If one thing can be guaranteed into the early part of next century it is expansion of man-modified landscapes. This will be a natural consequence of increases in numbers of humans and the consequent need for land to provide more living space, food, and fuel.

Our species has just reached 5,000 million individuals and by the year 2000 should stand at about 6,000 million. A peak of perhaps as many as 15,000 million early in the twenty-second century has been frequently forecast, although the Global 2000 study suggested a peak as high as 30 billion (Barney, 1980). Technology may allow production of more food and fuel on less land and may reduce pollution levels in the future, thus slowing the rate of habitat loss. Methods for habitat rehabilitation are being developed. But there will be an unavoidable time lag in application of such technology. A significant factor will be the availability and cost of appropriate technology. Largest population increases are in the many countries that total only an 18% share in world expenditure on research and development (Myers, 1984b). Economics may dictate hard choices regarding the

amount of pristine habitat and wilderness that each country can afford.

In regions that are highly modified through human influence, five particular factors can profoundly affect wild populations.

1) First, the landscape becomes "frozen in place" as attempts are made to control such natural processes as floods, fires, predation, and erosion so that their effects become minimal in a static pattern of towns, roads, farms, orchards, and remnant nature reserves. This can have serious consequences for many species. They can no longer move from one site to another in a continual pattern of local extinction and recolonization. Species become attuned to patterns and magnitudes of natural disturbance and stress, which are likely to be drastically altered in highly modified ecosystems.

Orothamnus zeyheri—a monotypic genus of the Proteaceae from South Africa—is just one example. For many years botanists had condemned the destructive effects of fire on the Cape Flora, resulting in fire protection. Investigation showed that this policy resulted in the decline of many species, including *Orothamnus*, which was reduced to 34 plants in four sites by 1968. Research showed that the species has natural cyclical fluctuations dependent on intervals between fires, with an optimum periodicity of 15 years for firing (Boucher, 1981).

One of the consequences of fragmentation of the landscape into a static pattern of land use is that conservation must become an integral part of land planning. There is also need for adequate mitigation processes and flexible options for preservation. Conservation of islandlike patches of habitat with narrow-range endemics in the San Bernardino Mountains of California, U.S.A., (Krantz, 1987), involved negotiation with five governmental agencies over ten years as well as detailed biological assessment and identification of key sites. A key device in this exercise is a regional biotic resources map, which assists selection of the best and most manageable sites for protection.

2) The second factor is isolation of patches of suitable habitat. Connecting corridors that facilitate gene flow, seasonal movement, and migration are lost.

3) The third factor is reduction in size of suitable areas of habitat. This has two main consequences. Some sites become so small that they are dominated by edge effects, and no undisturbed core habitat remains. Species in need of such core habitat die out and their place is taken by opportunist plants. The second consequence is reduction in population size so that random stochastic forces place the population at risk.

4) The fourth factor is increased competition with weeds. In a consultant's report to the last IUCN/WWF Plant Advisory Group meeting, although Cronk (1988) identified invasive weeds as an extremely serious environmental problem, he pointed out that "there is an extraordinary information vacuum where invasive plants are concerned." Similar conclusions were reached 1987 by a workshop on botanical management of the Galápagos Islands. There, such plants as *Cinchona succirubra* (quinine), *Lantana*, and the common guava threaten endemic plants of these unique oceanic islands (Adsersen, 1989).

5) Related to this is the fifth factor: predation. The effects, sometimes disastrous, of exotic herbivores on island floras is well documented. Today, predation by a wide range of animals, including goats, pigs, deer, chamois, and feral sheep and cattle, is a serious problem in many parts of the world. But smaller and sometimes overlooked organisms, such as fungi and viruses, can also have significant effects on plant populations. Disease transference from cultivation crops or nursery-propagated stock to wild plants must be guarded against, especially when executing recovery programs on oceanic islands. Cucumber mosaic virus has been detected in cultivated plants of the notable Chatham Islands endemic *Myosotidium hortensia*. Transfer of the virus to wild populations could have serious consequences for the species. Similarly, transfer of *Phytophthora cinnamonii* into previously uninfected areas can be a risk without stringent hygiene.

In landscapes highly modified by human activity there is special need for a series of key indicators of population health. These could collectively suggest which extinction vortices are involved, and the immediate and long-term remedial action required to prevent extinction. Halting population decline to low levels will be a critical aspect of this.

Plantations of exotic plants for timber and wind shelter have been neglected as potential havens for other plants. Yet, sometimes they can contain a surprisingly diverse and rich flora. In South Africa substantial populations of endangered members of the Cape fynbos flora have been found in pine plantations. In New Zealand the Iwitahi Reserve has been established in a mature stand of *Pinus nigra*. Twenty-seven species of native orchids are found here, including *Chiloglottis gunnii*, which is classed as vulnerable in New Zealand (Gibbs,

1988). Such habitats must not be regarded as necessary substitutes for undisturbed sites. But their potential role in conservation, especially in highly modified, peri-urban lowland regions, has been underestimated.

In highly modified landscapes interventionist management is unavoidable, and the objectives of such intervention need to be unambiguous. For many plant communities—especially in temperate regions—high and low levels of disturbance are likely to lead eventually to low levels of species diversity, which may be the natural state. However, if biodiversity is maximized in a particular region (especially given the fragmentary nature of many habitats), communities may have to be perturbed to promote the development of "unnatural" species-richness. It may be that some "naturalness" has to be sacrificed in the short term in order to maximize biodiversity.

Adequate and Appropriate Resources

Global expenditure on science and technology is very unevenly distributed. Approximately 82% of the effort on science and technology is in the developed nations with 20% of the population. The global communications system is controlled by those same countries (Myers, 1984b). Regions with the greatest need for scientific expertise may have least access to it. A critical evaluation of floristic knowledge in Latin America and the Caribbean by Toledo (1985) pointed out that this region has perhaps the world's greatest botanical diversity. Yet it lacks the indigenous resources to inventory fully and conserve that diversity. The 27 countries involved have over 900 resident botanists, but this contrasts with the 1,500 amateur and professional botanists in Great Britain alone. Colombia has an estimated 45,000 vascular plant species but only 47 resident botanists in 1985, and in 1981 had fewer than 350,000 plant specimens in its herbaria. A counter to this is the considerable botanical investment in Latin America by agencies such as Missouri Botanical Garden, Field Museum, New York Botanical Garden, and WWF (US). Nevertheless, Toledo concluded that the urgent need to inventory the great wealth of New World plants, the accelerated rate of habitat destruction, and limited resources implies: "collecting and correctly inventorying the greatest number of species possible in the least amount of time, that is, an endeavour which Fosberg once called a 'salvage botany'."

A second problem is that we are inundated by a flood of knowledge. Words flood the world and the entry of data processing in the 1970s seems to have done little to control and systematize the flow of information. Most scientists and managers know the problem of always seeming out of date, even in the most limited subject. Despite the most rigorous library and data base searches, there are always new papers and bulletins being published, journals that one cannot access, and incidentally discovered unpublished reports. New journals and newsletters are being proliferated at a rate that taxes the ability of most libraries to keep up to date. Language provides a barrier, and there is too little contact between scientists with different primary languages.

The effects of the information flood are compounded by a third problem—the subjection of science to marketplace economics. In the most ruthless form of free-market enterprise, science becomes a tradable commodity expected to return a profit to its financiers. This can result in a scramble for funds with competition between formerly cooperating departments of state, universities, and research organizations. The "free market" philosophy in science has "somehow changed the role of scientific enquiry in our society to a materially driven pursuit which is indistinguishable from marketing, labour relations, product development or pollution control. It is a key component of an industrial society. But it is much more than that. [. . .] it is very important that our citizens—particularly our young people—appreciate the cultural and intellectual significance of scientific enquiry" (Upton, 1988).

Transformative values in science have been a driving force in scientific investigation throughout civilized history. Conservation biology is not just to determine the best way to preserve biodiversity so that we can use it better, faster, and more efficiently—it also serves to open to our minds a world that is infinitely varied and has inspired poets, writers, and thinkers through the ages.

Stringent curbs on conservation expenditure, such as are occurring in many countries, can place the scientist and manager in an invidious position. Which species are allocated money for research and preservation? Can predator and weed control be undertaken? Are botanic gardens a luxury? Should limited resources be used to buy areas of wild habitat? When the choice is jobs or species preservation, which goes first? Problems of resource allocation are unlikely to improve in the near future unless there is a drastic change in attitudes toward nonhuman species. Increasing numbers of people and greater demands on space will mean less space for wild plants and animals, and diminished resources for conservation.

Conservationists of the future may be faced with the problem of triage: having to determine which species will slide toward extinction because there are insufficient resources to save them, which are not yet in need of urgent attention, and which can be treated with existing resources. It is tempting to put large amounts of time and money into a small number of spectacularly endangered species with public appeal while allocating little to species with less appeal or that are becoming critically endangered. In terms of conservation of overall biodiversity, it might be better to spend more on preventing species from reaching critical levels of endangerment.

Communication and Cooperation

Cooperation means assessing the strengths and weaknesses of contributing people and organizations, and then making the best use of each other's strengths and countering their weaknesses. It means maximizing use of resources, especially where these are scarce. At the simplest level it may also mean using the same vehicle to get researchers from different agencies onto field sites; at more complex levels it may mean closely integrating research and management programs and sharing major resources, such as herbaria, gardens, and laboratories. The need for cooperation exists at all levels from local and regional to national and international.

The trend toward an increasing degree of specialization and a view that "only engineers are qualified to talk about engineering, only biologists can talk about biology . . . etc." can result in a dearth of people who can bring such disciplines together cooperatively. There can also be unwillingness for people to speak to others outside their own speciality or to question the assumptions and conclusions of these other specialists. Yet we all need to question and understand viewpoints from other disciplines and cultures.

National and international organizations have a major contribution to make in promoting cooperation and good communication. The setting up of the joint IUCN-WWF Plant Advisory Group is just one of several positive moves to achieve this, but it is essential that such groups be in touch with what is actually happening in the "real" world. The urgent need in conservation is hands-on botanists and managers rather than desk-top administrators and prophets. Cooperation, especially in tropical countries, means involvement of local people, "grassroots support," rather than grandiose schemes run by expatriots. It is important that indigenous people and their knowledge be involved in setting up and managing nature reserves, restoration of habitat, and maintenance of sustainable forms of agriculture. Examples in Gradwohl & Greenberg (1988) show that through communication and cooperation, wise use and preservation of biodiversity can be achieved.

For most of the last two years I have been working on a global synthesis of the principles and practice of plant conservation. The project is both challenging and frustrating. One of the greatest pleasures has been to communicate with and learn from many hundreds of people, some working in the most out of the way places. It is a humbling experience, yet frustrating because many of these people with such good ideas and relevant experiences do not get the chance to share with others as they should. In many instances they do not have the resources to attend conferences and workshops outside their region; in other instances they are too busy performing practical conservation.

Innovation and Boldness

Two things that may determine much of the effectiveness of future conservation are innovation and boldness. If the situation in the early part of next century approaches worst-case scenarios, every bit of innovation and boldness may be needed to avoid vast numbers of extinctions, especially in the tropics.

A novel extension of the botanic garden concept is the idea of setting up a "Noah's Ark" refuge for species, especially for the establishment of plantations of northern hemisphere trees threatened by acid rain. This has been suggested several times in the last five years for isolated countries, such as New Zealand, where pollution is relatively low, and land is available. There are problems: are whole communities or ecosystems to be shifted to their new island home? Who pays? Will some introductions adversely affect indigenous plants through competition or introduction of new predators? Will expenditure on such a "Noah's Ark" downgrade efforts to conserve indigenous species? An overall problem is the question of "how long" will the ark have to accommodate species from defunct habitats? It is one thing to assume that ex situ conservation on a massive scale is permanent, but quite another to regard it as a temporary expedient for several decades (or even a century) until suitable habitats can be rehabilitated or created.

Establishment of new populations of plants in quasi-natural sites where they have not formerly occurred is similar to the "Noah's Ark" concept.

It may be justified where predation makes it impossible to preserve a species in its former habitat. The transfer of animals and plants to goat- and rat-free off-shore islands is an example of this. Another situation where it may be justified is where each population is reduced to only one sexual state, and the most reasonable chance for sexual reproduction is to establish a completely new population with a mixture of plants from remaining sites. New Zealand's *Gunnera hamiltonii* provides an example, being known from only four single-sex populations.

In some extreme instances the genome of exceedingly rare species might be transferred into related and more common species, either through hybridization or genetic engineering. This brings into question the ultimate goal of conservation: whether the preservation of species or of biodiversity. If the latter, then one can argue that it matters less how valuable genes are preserved than that they be preserved somewhere and somehow.

There are various ways in which in situ and ex situ approaches can be combined to make persistence of a small population more likely. One technique might involve maintenance of some areas of suitable habitat and harvesting of seed, sampled to maximize genetic diversity. Some of this seed would be banked for long-term storage as a precautionary measure against catastrophe, while some would be used for garden propagation and replanting back into the wild site. In effect, population size is maintained above a critical level by a combination of in situ preservation in the wild and ex situ preservation in gene banks, laboratories, and botanic gardens.

If models of global warming through the "greenhouse effect" are valid, every scrap of ingenuity may be needed to conserve biodiversity in the twenty-first century. Although some aspects such as sea-level rise and fluctuations in ocean and atmospheric circulation are hotly debated, it is not too early to consider possible scenarios and their implications for conservation. Climatic shifts will have a number of serious consequences (Peters, 1988). Changes in species distribution can be expected as conditions become locally unsuitable for persistence. In some long-lived species, although adult plants may remain, this will result in a regeneration gap, especially where germination or seedling growth requires seasonal chilling. Spectacular initial losses are likely to involve arctic-alpine species at relictual sites, such as *Rhododendron lapponicum* at Wisconsin Dells or the postglacial disjuncts along the north shore of Lake Superior (Given & Soper, 1981).

For many species the choice will be to migrate or be extirpated. But suggested rapidity of climate change means that migration rates required will exceed natural migration rates for many species. Today's fragmented landscape offers a formidable obstacle course to migrating species. Peters (1988) gave the example of *Picea engelmanii*, which would require over 1,000 years to adjust its range to a new climatic regime.

To mitigate climatic change requires several courses of action (Peters, 1988; Myers, 1984b). Refinement of "greenhouse" models is urgently needed, and selected species in regions where early effects can be detected should be monitored without delay. Preservation of representative populations throughout the whole range of species is another strategy; often there has been a tendency to be satisfied with one reserve for a species. In all reserves there need to be contingency plans for modification of drainage and irrigation to allow for changes in moisture regimes. Changes in weed and predator distribution are likely and could profoundly affect some species. This requires early identification of such problems. It makes sense to locate new reserves at the poleward end of species ranges (because of poleward retreat of temperature-sensitive species). Particular reserves should maximize diversity in habitats and altitudinal gradients.

At least in the short term, an important role must be assumed by botanic gardens and gene banks to ensure that plant diversity that may have difficulty surviving in the wild is preserved. This challenge needs to be taken up at all levels, from the local garden and research center to international organizations such as IUCN and IBPGR.

The limitations of ex situ conservation have been pointed out by Foose (1986) with respect to animals. He argued that the capacity of the "zoo ark" to cope with at least 1,500 mammals, birds, reptiles, and amphibians expected to be endangered by the middle of next century is very limited. As a consequence, the American Associaton of Zoological Parks and Aquariums has designated through its Species Survival Plan 37 priority taxa for ex situ preservation. The eventual aim is to have up to 1,000 species designated. However, this will still fall far short of requirements for the next century.

Similarly, it is debatable whether botanical gardens and gene banks can eventually guarantee the persistence under ex situ conditions of their share of the world's biota, at least without a great deal of reorganization. If the number of botanic gardens could be doubled and each persuaded to take prime responsibility for ten different plant taxa under threat, we would be a long way toward shepherding

the flora of the world through the problems of next century. There have been numerous criticisms of botanic gardens and gene banks in recent years and whether their long-term role for conservation is outweighed by their deficiencies. Most of the problems cited, such as poor documentation and lack of adequate regenerative procedures for seeds, are not a reflection of fundamental problems so much as the result of poor management, unclear objectives, and inadequate finance. These are all capable of correction, provided there is a change in the fundamental attitudes of society to biological conservation.

Rediscovering an Ethic

It is easy to make facile appeals to new technology to solve environmental problems, and there is no doubting the contribution of such advances as satellite imagery to conservation today. But no amount of technology or innovation will sustain plant diversity into the future unless there are fundamental changes in attitudes to biodiversity. This means moving away from exploitation and toward sustainable systems, changes in economic systems dominated by benefit-cost analysis (BCA), acknowledging the place of nonutilitarian values such as intrinsic and transformative values (Norton, 1988), greater social justice, and equity in resource distribution. Progressively more intensive applications of science and technology to Western society, requiring increased levels of energy consumption as well as larger and more centralized structures and institutions, have increased stress in environmental and social systems in ways not reflected in conventional analyses (Dahlberg, 1987). Although lip service is paid to conservation, "In the pursuit of economic gain, most people do not want to be bothered by questions of biodiversity" (Cobb, 1988).

Is biodiversity misunderstood even by members of the scientific community who ought to be its champions? David Ehrenfeld (1986b) suggested that ecologists have been "co-opted by economists" because it is difficult for the former not to respond to arguments based on fundamental scientific misconceptions and, more important, because of the compelling power in Western society of arguments based upon numbers and resources. He contended that "most of us, apart from a few hard-core philosophers, suffer from a deep-seated fear of economists" and challenged scientists themselves to "recapture the love of diversity for its own sake."

We live in a global commons where there needs to be mutual interdependence and not independence. We need a new understanding of natural sources and resources based on a hierarchy where "genetic and biological diversity are more fundamental than renewable resources, which in turn are more basic than nonrenewable resources" (Dahlberg, 1987). It is too tempting for individuals and institutions, especially those of the developed Western countries, to be "free riders" in the global system, ignoring limits to growth and assuming that just around the corner yet another bit of technology will solve the present crises. The irony is that some of the indigenous people who may be displaced from their traditional lands by the "free riders" are the very people who have learned to live in harmony with their environment, utilizing yet conserving the plants around them. No culture can afford to be so arrogant that it ignores the cultural and technological systems of others.

Do doomsday messages cut any ice? A few days ago a letter appeared in the Christchurch *Press* following the suggestion by geologists that there was a high risk of a severe earthquake:

> Sir [. . .] This is the second, in as many days, of this kind of depressing report. It is bad enough to be bombarded daily with the horrible realities of present unemployment, inflation, crime, etc., but to have to hear of the future in such a negative way is just too much. The morale of our country, with its present problems, is low and this sort of unnecessary sensationalism in our daily papers does not help it. Why not give us articles about the positive things "likely" to happen. . . .

This has been described as the Cassandra problem, an allusion to the Greek prophetess Cassandra whose prophecies were true but not believed by their hearers. Les Kaufman (1986) pointed out that: "To some people, these Cassandras, as they call themselves, are professional doomsayers, intellectual terrorists who should not be encouraged, supported, or believed. What seems to have escaped such doubters, however, is that the whole point of being a doomsayer is to agitate the world into proving you wrong or into doing something about it if you are right."

There is no lack of publications arguing the case for a change of attitude to natural resources and a new stewardship of biological diversity. A research agenda suggested by Myers (1986b) outlines nine topics as priorities for research, including extinction links, vulnerability of systems and taxa, rates of recovery from depletion, and the economics of threatened species. A study of ecological aspects of development in the humid tropics (National Research Council-US 1982) sets out a similar agenda for use of tropical resources. That govern-

ments and institutions seem to have difficulty implementing many such agendas seems to suggest that we do have a Cassandra problem, and that the difficulty is not so much one of ignorance but lack of will and commitment.

It is tempting to yield to "doom and gloom" scenarios and to give up. On the other hand, the gathering of nearly 800 participants in November 1986 to discuss conservation and management of rare and endangered plants in California, U.S.A., shows that interest in plant conservation can and should be generated (Elias, 1987). Myers (1988a) has pointed out that, despite the gloomy prognosis for many of the world's species, given the will, the means are available to stem the tide of extinction. He calculated the cost of an Action Plan to promote intensified stable agriculture, halt spread of deserts and depletion of rainforests, supply family planning services throughout the Third World, and provide clean water to 1.5 billion people as $67 billion (U.S.) a year. This is less than twice as much as current development aid. Norman Myers asks not "Can we afford to do it?" but "How can we afford not to do it?"

It seems reasonable to express optimism that the worst scenarios are unlikely to occur and we can hope for sanity and "common sense" to prevail. Is it too much to hope that by the year 2100, McNeely's (1986) scenario of a world no longer needing national parks will be a reality? As he pointed out, national parks and other protected areas are an admission that people have not learned to live with nature or are forced to live with nature.

A change to a conservation-oriented world means a commitment to social justice and equity on a global scale. It means (Raven, 1986): "an awareness of and compassion for all life, and an appreciation of the fact that we are all part of a living world. [. . .] we should not allow ourselves to respond only when the crises that we have caused are so extensive that they threaten our lives. To do so is to be thoroughly immoral in the fullest meaning of the word." To change means opening people's eyes to the positive aspects of nature; yet it also means being honest and realistic about the risks to biodiversity. The greatest danger may not be that biodiversity will be lost in a sudden cataclysm precipitated by *Homo sapiens* but that we will allow planet Earth to die by attrition. In James A. Michener's novel *Caravans*, the question is asked of a ruined desert city: "Why did it die?" (Michener, 1964). We are told: "[. . .] this used to be the world's foremost example of irrigation. [. . .] But people got lazy. They didn't keep working on it. They felt that what had worked for a hundred years was good enough for the next hundred years. They stopped building the ditches [. . .] built no new dams. They guessed right. For a hundred years, no trouble. But the death warrant had been signed." We need to ensure that the death warrant is not signed for Earth—even by default.

Conservation has a message for the world about plant diversity. But for the world to take notice may depend on heeding the advice of General Booth, founder of the Salvation Army, who pointed out that if you present good news to a starving man then you must wrap it in a sandwich. The tragedy we face through the loss of plant diversity may mean that very soon we may have tens of millions of starving people but very few sandwiches.

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INTRODUCTION

A SYMPOSIUM ON THE BIOLOGICAL DIVERSITY AND EVOLUTION OF THE TARWEEDS

The tarweed subtribe Madiinae of the sunflower tribe Heliantheae is a highly diversified, yet cohesive group of 17 genera and 127 species, with centers of diversity in California and Hawaii. In California, the tarweeds received the attention of such pioneers in biosystematics as H. Hall, E. Babcock, and the team of J. Clausen, D. Keck, and W. Hiesey. The results of these early workers significantly influenced the way succeeding generations of botanists viewed the evolutionary divergence of plant populations. In Hawaii, the tarweeds became known for their spectacular adaptive radiation into a tremendous variety of habitats and growth forms. Thus, the tarweeds have provided an excellent means for studying the processes of biological diversification in continental and insular ecosystems. A symposium exploring the biological diversity and evolution of the tarweeds was sponsored by the American Society of Plant Taxonomists and the Botanical Society of America and was held in Davis, California, at the American Institute of Biological Sciences meeting in August 1988. The symposium was dedicated to Sherwin Carlquist in recognition of his outstanding contributions to tarweed research. The following papers stem from the symposium and summarize current research aimed at understanding diverse aspects of this fascinating group of plants.

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ADAPTIVE RADIATION OF THE HAWAIIAN SILVERSWORD ALLIANCE (COMPOSITAE–MADIINAE): ECOLOGICAL, MORPHOLOGICAL, AND PHYSIOLOGICAL DIVERSITY[1]

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Abstract

The ecological, morphological, and physiological diversity of species in the Hawaiian silversword alliance is exceptional. The 28 species, which belong to the endemic genera *Argyroxiphium*, *Dubautia*, and *Wilkesia*, have a wide variety of geographical distributions and elevational ranges within the archipelago. They grow in habitats as varied as dry scrub and woodland, wet scrub and forest, cinder and lava, and bog. Ecological diversity is also evident among sympatric species. At a site of sympatry on the island of Hawaii, for example, *D. ciliolata* and *D. scabra* are restricted to different lava flows, even though individuals of the two species may grow within a meter of one another. The 28 species have growth forms as varied as rosette shrubs, shrubs, trees, and lianas. They have a wide range of leaf sizes and shapes, with the *Dubautia* species exhibiting significant variation in leaf turgor maintenance capacities. Morphological and physiological diversity is also evident among sympatric species. At a site of sympatry on the island of Maui, for example, *A. sandwicense* and *D. menziesii* exhibit different suites of morphological and physiological traits enabling them to cope with the severe environmental conditions. The patterns of diversity and the genomic relationships among the 28 species suggest that a variety of factors may have played important roles in their adaptive radiation.

The Hawaiian silversword alliance is a premier example of adaptive radiation in plants (Carlquist, 1980; Carr et al., 1989). The alliance includes 28 species in three endemic genera: *Argyroxiphium*, *Dubautia*, and *Wilkesia* (Carr, 1985). The species grow in a wide range of habitats and have a wide variety of growth forms. They are also closely related, as evidenced by the high frequency of spontaneous interspecific and intergeneric hybrids in nature, coupled with the ease of production of artificial hybrids in the laboratory (Carr & Kyhos, 1981, 1986). The detailed analysis of the hybrids and parental taxa using cytogenetic, electrophoretic, and molecular approaches has provided compelling evidence that the silversword alliance is a genetically cohesive group whose origin and diversification probably trace to a single colonizing ancestor (Baldwin et al., 1988; Carr et al., 1989).

Our objective in this review is to provide insight into the ecological, morphological, and physiological diversity of species in the silversword alliance. With respect to ecological diversity, we compare the geographical distributions, habitats, and elevational ranges of the 28 species, then analyze the local distributions of several sympatric *Dubautia* species. With respect to morphological and physiological diversity, we compare the growth forms, leaf sizes, and leaf shapes of the 28 species, then examine the turgor maintenance capacities of the *Dubautia* species and the water and temperature balances of two sympatric *Argyroxiphium* and *Dubautia* species. Our primary theme is that the

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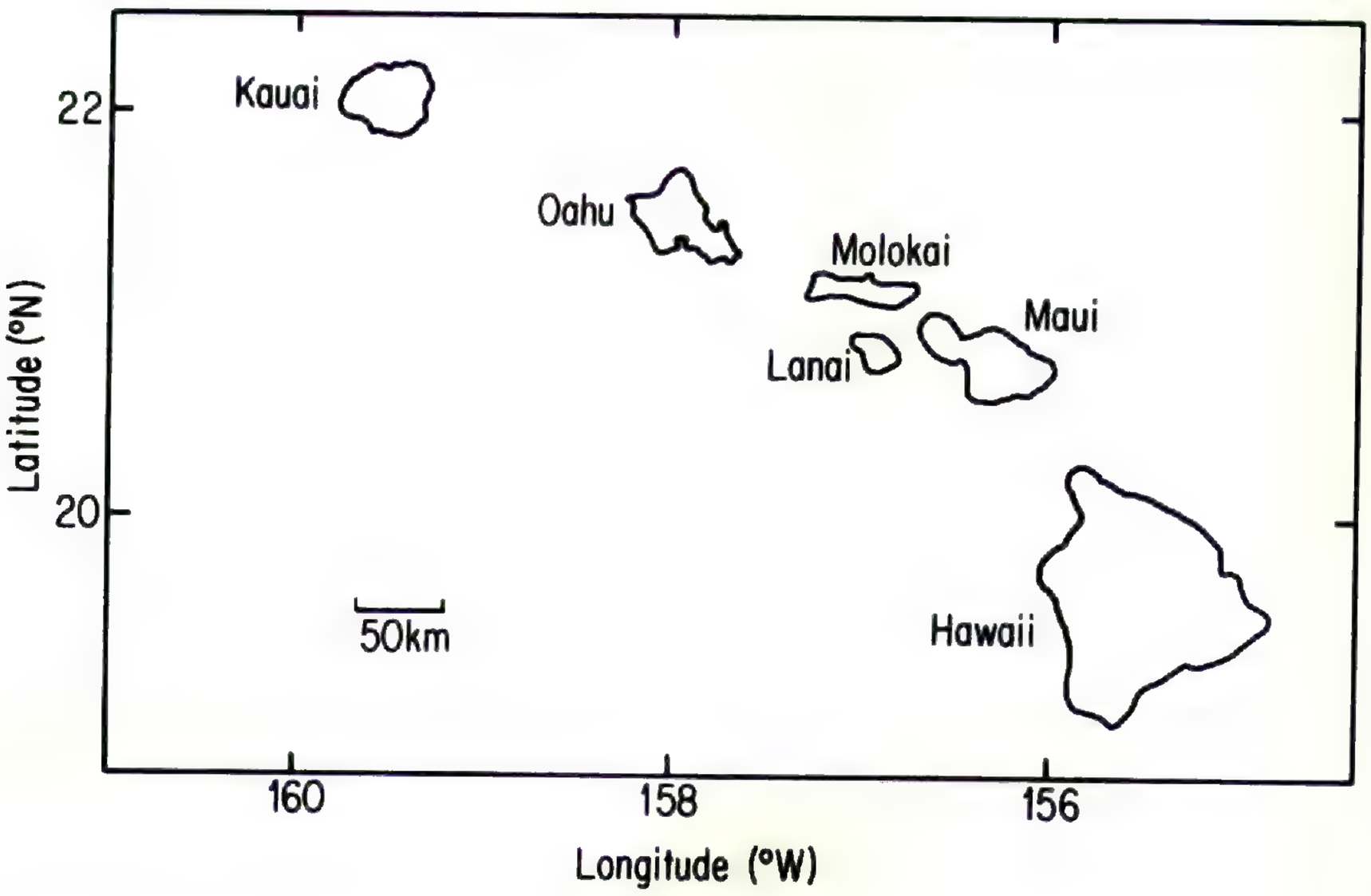

FIGURE 1. Major islands of the Hawaiian archipelago.

ecological, morphological, and physiological diversity of the species is exceptional. Understanding the pattern and significance of this diversity, together with the factors giving rise to it, provides a key to understanding adaptive radiation in plants.

ECOLOGICAL DIVERSITY

The Hawaiian archipelago includes six major islands (Fig. 1). Maui, Lanai, and Molokai, which are currently separated by shallow channels, were united into one large island during periods of lower sea level in the Pleistocene (Macdonald & Abbott, 1970). Thus, they function as a single biogeographic unit known as the Maui complex (Carson & Kaneshiro, 1976; Simon, 1987). The ages of the islands increase progressively from southeast to northwest. Based on potassium–argon dating, the ages of older sections of the islands, in millions of years, are: Hawaii—0.7, Maui—1.3, Lanai—1.5, Molokai—1.8, Oahu—3.3, and Kauai—5.6 (Macdonald & Abbott, 1970).

Species in the silversword alliance have significantly different geographical distributions within the archipelago (Table 1). All *Argyroxiphium* species, most 13-paired *Dubautia* species, and one 14-paired *Dubautia* species are confined to Hawaii, the Maui complex, or both. Most 14-paired *Dubautia* species and both *Wilkesia* species, in contrast, are confined to Kauai. Two 13-paired *Dubautia* species are restricted to Oahu, and two 14-paired species grow on Kauai, Oahu, and at least one of the younger islands. Of the latter species, only *D. plantaginea* grows on all major islands.

The archipelago supports a wide variety of terrestrial habitats. The habitats containing species in the silversword alliance are grouped into four broad categories in Table 1. The dry scrub and woodland habitat has low annual rainfall with a prolonged dry season. The vegetation ranges from low, open scrub dominated by deciduous and evergreen shrubs to taller woodland with scattered deciduous and evergreen trees. The wet scrub and forest habitat has medium to high annual rainfall without a prolonged dry season. The vegetation ranges from tall, closed forest with a high diversity of evergreen trees to lower, more open forest and scrub dominated by the evergreen *Metrosideros polymorpha* (Myrtaceae) and rich in epiphytic bryophytes and pteridophytes. The bog habitat has very high annual rainfall, waterlogged, acidic soils, and stunted vegetation. The cinder and lava habitat has low or high annual rainfall, exposed volcanic substrates with very limited soil development, and sparse vegetation. The range in annual rainfall among the four habitats, from less than 400 mm to more than 12,300 mm, is exceptional.

Species in the silversword alliance have significantly different distributions among the four habitats (Table 1). One *Argyroxiphium* species, six 13-paired *Dubautia* species, and both *Wilkesia* species grow in the dry scrub and woodland habitat. Most *Argyroxiphium* species, four 13-paired *Dubautia* species, and all 14-paired *Dubautia* species, in contrast, grow in the wet scrub and forest habitat, the bog habitat, or both. In addition to growing in other habitats, five species grow in the cinder and lava habitat, where they are among the first

TABLE 1. Ecological and morphological characteristics of *Argyroxiphium*, *Dubautia*, and *Wilkesia* species. Nomenclature and diploid chromosome pairs derive from Carr (1985). Ecological and morphological data derive from the analysis of approximately 2,000 herbarium specimens (Carr, 1985) and from extensive field research. Islands are: H = Hawaii, K = Kauai, M = Maui complex, and O = Oahu. Habitats are: b = bog, c = cinder and lava, d = dry scrub and woodland, and w = wet scrub and forest. Growth forms are: l = liana, r = rosette shrub, s = shrub, and t = tree. Leaf lengths are ranges for mature leaves from dried specimens.

Species	Chromosome pairs	Island	Habitat	Elevational range (m)	Growth form	Leaf length (mm)
Argyroxiphium caliginis	14	M	b	1,350–1,650	r	35–150
A. grayanum	14	M	b	1,200–2,050	r	50–310
A. kauense	14	H	b	1,625–1,900	r	200–400
A. sandwicense	14	H, M	d, c	2,125–3,750	r	130–390
A. virescens	—	M	w	1,600–2,300	r	170–300
Dubautia arborea	13	H	d	2,125–3,100	s, t	30–90
D. ciliolata	13	H	d, c	900–3,200	s	5–30
D. dolosa	13	M	w	1,525–2,275	s	40–120
D. herbstobatae	13	O	d	580–925	s	20–55
D. linearis	13	H, M	d, w, c	450–2,500	s	10–75
D. menziesii	13	M	d, c	1,800–3,075	s	20–50
D. platyphylla	13	M	d	1,725–2,750	s	40–90
D. reticulata	13	M	w	1,575–2,300	s, t	30–70
D. sherffiana	13	O	w	600–1,150	s	25–100
D. imbricata	14	K	w, b	700–1,550	s	60–150
D. knudsenii	14	K	w	550–1,375	s, t	50–220
D. laevigata	14	K	w	575–1,250	s	70–240
D. latifolia	14	K	w	975–1,200	l	80–170
D. laxa	14	M, O, K	w, b	350–1,700	s	40–200
D. microcephala	14	K	w	825–1,275	s	100–240
D. paleata	14	K	b	1,100–1,550	s	35–200
D. pauciflorula	14	K	w	700–725	s	80–210
D. plantaginea	14	H, M, O, K	w	300–2,100	s	80–260
D. raillardioides	14	K	w	600–1,375	s	90–250
D. scabra	14	H, M	w, c	75–2,500	s	10–90
D. waialealae	14	K	b	1,450–1,600	s	10–30
Wilkesia gymnoxiphium	14	K	d	425–1,100	r	150–500
W. hobdyi	14	K	d	275–400	r	100–200

vascular plants to colonize the exposed volcanic substrates. The most widespread species ecologically is the 13-paired *D. linearis*, which grows in the dry scrub and woodland habitat, the wet scrub and forest habitat, and the cinder and lava habitat.

Elevations in the archipelago extend from sea level to 4,206 m (Mueller-Dombois, 1981). Species in the silversword alliance collectively span most of this elevational gradient, growing from 75 m to 3,750 m. The species have a wide variety of elevational ranges, however, with no two species having the same range (Table 1). *Dubautia pauciflorula* and *D. waialealae*, for example, have narrow ranges, whereas *D. ciliolata* and *D. scabra* have wide ranges. In addition, *D. herbstobatae* and *W. hobdyi* have ranges restricted to low elevations, whereas *A. sandwicense* and *D. arborea* have ranges restricted to high elevations. At low elevations minimal daily temperatures rarely drop below 15°C. At high elevations, in contrast, minimal daily temperatures may drop below 0°C for extended periods, especially during winter months.

At many localities in the archipelago, species in the silversword alliance grow sympatrically. In several instances, the sympatric species exhibit local distributions that differ markedly. *Dubautia ciliolata* and *D. scabra*, for example, grow sympatrically at a site on the upper slopes of Mauna Loa, Hawaii. The site is covered by exposed lava from past eruptions of Mauna Loa. Most of the site is covered by pahoehoe lava from a 1935 eruption. This younger flow is discontinuous in places, however, such that lava from a prehistoric flow is exposed. The older flow consists of a mixture

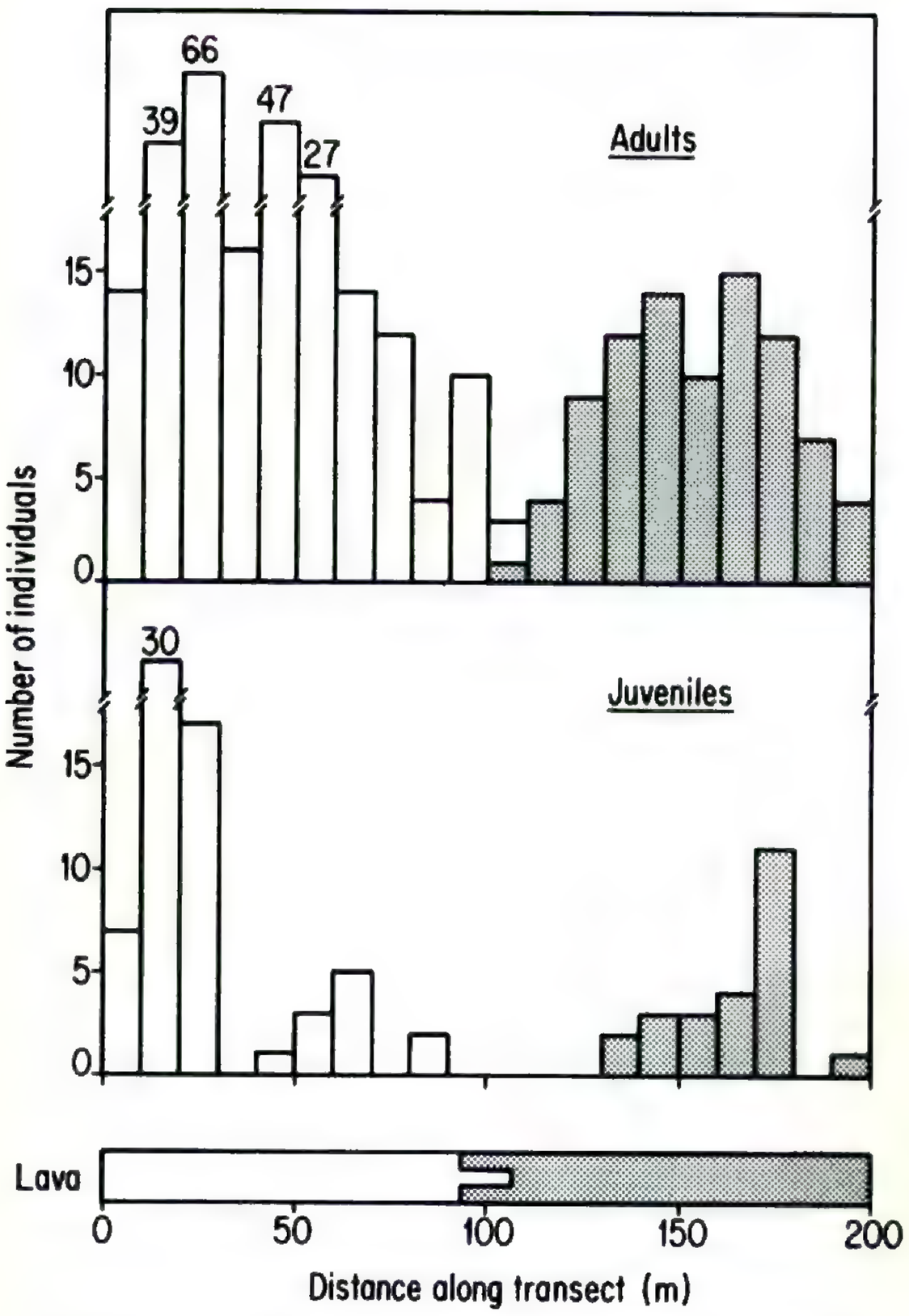

FIGURE 2. Distributions of adults and juveniles of *Dubautia ciliolata* and *D. scabra* at a site of sympatry on Mauna Loa, Hawaii. The site was located at 1,980 m near Puu Huluhulu along the Saddle Road (Robichaux, 1984). The 200-m-long, 10-m-wide transect crossed two lava flows. The first 100 m crossed an older flow of pahoehoe and aa lava; the second 100 m crossed a younger flow of pahoehoe lava. In the zone of interdigitation at 95–105 m, fingers of the younger flow covered sections of the older flow. At points of contact in this zone, the transition from one flow to the other was very abrupt. Adults and juveniles were defined as individuals with crown diameters greater than and less than 20 mm, respectively. In both species, large adults had crown diameters exceeding 1 m. For the number of individuals along the transect, the unshaded and shaded bars denote *D. ciliolata* and *D. scabra*, respectively. For the distribution of lava along the transect, the unshaded and shaded sections denote the older and younger flows, respectively. The species distributions are significantly different for adults and for juveniles with chi-square tests at $P < 0.001$.

of pahoehoe and aa lava. At points of contact between the two flows, the transition is very abrupt, occurring over a distance of 1–2 mm. The pockets, or kipukas, of the older flow vary in size from less than 1 m^2 to more than 10,000 m^2. Thus, the landscape at the site is a mosaic of the two flows.

Though both *Dubautia* species are common at the site, their local distributions differ significantly (Fig. 2, Table 2). *Dubautia ciliolata* is almost completely restricted to the older flow, whereas *D. scabra* is completely restricted to the younger flow.

TABLE 2. Distributions of adults of *Dubautia ciliolata*, *D. scabra*, and their natural hybrid at a site of sympatry on Mauna Loa, Hawaii. The site is the same as in Figure 2. The oval-shaped sample area was approximately 350 m long and 150 m wide. It included a large pocket, or kipuka, of the older lava flow that was approximately 250 m long and 50 m wide. It also included a 50-m-wide section of the younger lava flow that completely surrounded the kipuka.

Taxon	Number of adults	
	Older flow	Younger flow
D. ciliolata	1,692	28
D. scabra	0	487
Hybrid	0	29

With regard to the small proportion of adult individuals of *D. ciliolata* that grow on the younger flow, over 80% are small plants that occur within 4 m of the boundary between the two flows. In this zone, the younger flow tends to decrease in thickness. Hybrids between the two species are also common at the site. Like *D. scabra*, they are completely restricted to the younger flow (Table 2).

The differential restriction of *D. ciliolata* and *D. scabra* to the two flows occurs for juvenile and adult plants (Fig. 2), suggesting that factors leading to the differential restriction may operate primarily during the stages of seed dispersal and seedling establishment. Both species produce very large quantities of small, light, wind-dispersed seeds each year, which appear to be readily dispersed across the two flows. Hence, seedling establishment may be the more critical stage.

The local distributions of *D. ciliolata* and *D. scabra* also differ at other sites of sympatry on Hawaii. At 1,125 m near Keanakakoi Crater on the slopes of Kilauea, for example, *D. ciliolata* is restricted to a 1959 cinder substrate and *D. scabra* is restricted to an adjacent 1974 pahoehoe lava flow (L. Stemmermann, pers. comm.).

Other sympatric species in the silversword alliance also exhibit different local distributions. *Dubautia paleata* and *D. raillardioides*, for example, grow in the Alakai Swamp region of Kauai. This large, dissected, upland plateau receives 6,000–10,000 mm of rainfall per year. The vegetation is composed primarily of wet forest, with a mosaic of bogs scattered over the more level areas. Though both species are common at sites of sympatry, *D. paleata* is largely confined to the bogs, whereas *D. raillardioides* is always restricted to the wet forest (Canfield, 1986).

Morphological and Physiological Diversity

Species in the silversword alliance have a wide variety of growth forms (Table 1). All *Argyroxiphium* and *Wilkesia* species are rosette shrubs, with some species being primarily monocarpic (e.g., *A. sandwicense* and *W. gymnoxiphium*) and others being commonly polycarpic (e.g., *A. grayanum* and *W. hobdyi*). The rosettes are sessile in some species (e.g., *A. caliginis*) and elevated on woody stems up to 5 m tall in other species (e.g., *W. gymnoxiphium*). Most *Dubautia* species are shrubs, though they vary from small, spreading forms (e.g., *D. herbstobatae* and *D. scabra*) to large, woody, erect forms (e.g., *D. dolosa* and *D. plantaginea*). Three *Dubautia* species commonly grow as small trees 5–8 m tall, with the woody trunks of large individuals of *D. arborea* and *D. reticulata* reaching 0.4–0.5 m in diameter. *Dubautia latifolia* is a liana that climbs into the canopies of large trees. Stems of *D. latifolia* often exceed 8 m in length and may reach 70 mm in diameter near the base.

Species in the silversword alliance also have a wide range of leaf sizes and shapes. In the extremes, leaf lengths differ by two orders of magnitude, ranging from 5 mm to 500 mm (Table 1). All *Argyroxiphium* and *Wilkesia* species have long, narrowly ligulate to linear leaves, with the leaves of *A. caliginis* being the shortest on average. With the exception of *D. scabra* and *D. waialealae*, the 14-paired *Dubautia* species tend to have longer leaves than the 13-paired species. Leaf shapes among the *Dubautia* species include elliptic, lanceolate, linear, ovate, oblanceolate, oblong, and obovate (Carr, 1985).

In addition to morphological diversity, species in the silversword alliance exhibit significant physiological diversity. Among the *Dubautia* species, for example, differences in chromosome number and habitat water availability are strongly correlated with differences in leaf turgor maintenance capacity (Robichaux, 1984, 1985; Robichaux & Canfield, 1985). The 13-paired species from the dry scrub and woodland habitat, such as *D. ciliolata*, *D. menziesii*, and *D. platyphylla*, have much greater capacities for maintaining high turgor pressures as tissue water content decreases than the 14-paired species from the wet scrub and forest habitat, such as *D. knudsenii*, *D. plantaginea*, and *D. raillardioides*. Their greater turgor maintenance capacities may play a key role in enabling the 13-paired species from the dry scrub and woodland habitat to tolerate conditions of low soil water availability.

Morphological and physiological diversity is also evident among species that grow in the same habitat. *Argyroxiphium sandwicense* and *D. menziesii*, for example, grow sympatrically in the alpine cinder and lava habitat of Haleakala, Maui, where environmental conditions are severe. Under the high solar irradiances characteristic of this habitat in summer, substrate temperatures are often very high during the day. Coupled with the low annual rainfall of 600–700 mm, these conditions appear to limit plant growth significantly, resulting in a landscape with very low vegetative cover.

The growth forms and leaves of *A. sandwicense* and *D. menziesii* differ significantly (Figs. 3–6). *Argyroxiphium sandwicense* is a monocarpic, rosette shrub with long, narrow, densely pubescent leaves, whereas *D. menziesii* is a polycarpic, woody, diffusely branched shrub with small, glabrous leaves. The difference in leaf pubescence results in a large difference in leaf absorptance. Leaf absorptances (0.4–0.7 μm) measured with an integrating sphere are 0.39 $\pm$ 0.01 (mean $\pm$ 1 S.E.; N = 5) in *A. sandwicense* and 0.80 $\pm$ 0.01 (N = 4) in *D. menziesii*. (The leaf absorptances are significantly different with a *t*-test at $P < 0.001$.)

The leaf water balances of *A. sandwicense* and *D. menziesii* during the middle of the summer growing season also differ significantly and are markedly influenced by the prevailing atmospheric conditions at Haleakala. On most July days, when the moisture-laden tradewinds blow from the northeast, a massive cloud bank forms around the mountain. The altitude of the cloud bank varies considerably from day to day, however, such that the atmospheric humidities to which *A. sandwicense* and *D. menziesii* are exposed also vary considerably. On 1 July 1985, for example, the upper ceiling of the cloud bank was 1,750–1,850 m throughout the day. As a result, atmospheric humidities at the study site (2,820 m) were very low, with the leaf-to-air vapor pressure gradient reaching 29 mPa Pa^{-1} in both species at midday (Table 3). On 5 July 1985, in contrast, the upper ceiling of the cloud bank was 2,650–2,750 m during much of the day. As a result, atmospheric humidities at the study site were significantly higher, with the vapor pressure gradient reaching only 15 mPa Pa^{-1} in both species at midday (Table 3; $P < 0.001$ for the difference between days in each species).

The large differences in vapor pressure gradients are paralleled by significant differences in leaf conductances to water vapor in both species (Table 3; $P < 0.001$ for the difference between days in each species). In *A. sandwicense* and *D. menziesii*, midday leaf conductances on 1 July 1985 were

FIGURES 3–6.—3. *Argyroxiphium sandwicense*.—4. *Dubautia menziesii*.—5. Leaves of *A. sandwicense* (upper) and *D. menziesii* (lower), with a nickel coin for scale.—6. Habitat of *A. sandwicense* and *D. menziesii* on Haleakala, Maui. For both species, the average height of mature individuals in the photograph is 0.6–0.9 m.

67.5% and 68.7%, respectively, of those on 5 July 1985. Thus in both species, a higher midday leaf conductance is correlated with a lower midday vapor pressure gradient. The correlations suggest a direct stomatal response to changes in the vapor pressure gradient, as has been reported in a large number of species from a wide variety of habitats (Schulze, 1986). Such stomatal responses enable plants to restrict water loss before severe water deficits develop.

Though the two species exhibit similar correlations between leaf conductances and vapor pressure gradients, midday leaf conductances are significantly higher in *A. sandwicense* than in *D. menziesii* (Table 3; $P < 0.001$ for the difference between species on each day). On 1 and 5 July 1985, midday leaf conductances in *A. sandwicense* were approximately twice as high as in *D. menziesii*. With its higher leaf conductances, *A. sandwicense* also exhibits significantly higher midday and daily leaf transpiration rates than *D. menziesii* (Table 3; $P < 0.001$ for the difference between species on each day). Thus, the total daily water use per unit leaf area of *A. sandwicense* appears to be much greater than that of *D. menziesii* in July.

Despite its higher transpiration rates, *A. sandwicense* does not exhibit markedly lower midday water potentials than *D. menziesii* (Table 3). This suggests that the two species may differ in rooting depths, and thus in access to available soil water supplies. Alternatively, they may differ in hydraulic resistances or capacitances. In contrast to *D. menziesii*, *A. sandwicense* accumulates very large amounts of extracellular polysaccharide in its mature leaves (Carlquist, 1957; Carr, 1985). In the related species, *A. grayanum*, the presence of this polysaccharide is correlated with a large increase

TABLE 3. Water and temperature balance parameters of *Argyroxiphium sandwicense* and *Dubautia menziesii* on 1 and 5 July 1985 at a site of sympatry on Haleakala, Maui. The site was located at 2,820 m along the summit road. Clear skies prevailed at the site on both days, with midday solar irradiances exceeding 1,020 W m^{-2}. Standard errors of the means are given in parentheses. Results of the relevant *t*-tests are provided in the text.

Parameter[1]	*A. sandwicense*		*D. menziesii*	
	1 July	5 July	1 July	5 July
Midday vapor pressure gradient (mPa Pa^{-1})	29.1 (0.1)	15.5 (0.1)	29.1 (0.4)	15.3 (0.3)
Midday leaf conductance (mmol m^{-2} s^{-1})	332.7 (4.5)	493.1 (4.3)	170.0 (11.6)	247.6 (7.8)
Midday leaf transpiration rate (mmol m^{-2} s^{-1})	8.7 (0.1)	6.6 (0.1)	4.7 (0.3)	3.5 (0.1)
Daily leaf transpiration rate (mol m^{-2} d^{-1})	276.2 (5.1)	234.8 (4.1)	158.0 (12.4)	113.3 (4.2)
Midday water potential (MPa)	−1.1 (0.1)	−0.9 (0.1)	−1.0 (0.1)	−0.8 (0.1)
Midday leaf temperature (°C)	19.6 (0.1)	17.7 (0.1)	19.5 (0.2)	17.6 (0.2)

[1] Parameters were measured for five individuals per species, with the ten individuals growing intermingled in an area of approximately 10 m radius. Except for water potentials, parameters were measured for 2–4 recently mature leaves per individual. Leaf and air temperatures were measured with 0.127-mm copper-constantan thermocouples connected to a Wescor Corp. model TH-65 digital thermocouple thermometer. Leaf conductances to water vapor were measured with a LI-COR Corp. model LI-1600 steady-state porometer. Both species were amphistomatous, with the upper and lower leaf surfaces contributing approximately equally to the total leaf conductances. In *A. sandwicense*, the measured leaf conductances included the effects of the dense, appressed pubescent layer. Leaf conductances were measured at 2–3-hr. intervals throughout the day, with each measurement sequence taking 0.3 0.7 hr. Midday leaf conductances were the maximal leaf conductances in both species. Boundary layer conductances to water vapor and leaf transpiration rates were calculated according to the equations in Nobel (1983). Wind speeds were measured with a hot-wire anemometer and averaged 1 m s^{-1} during the sampling periods. Atmospheric humidities were measured with the humidity probe in the porometer. Intercellular-air-space humidities were assumed to be saturated and were calculated from the measured leaf temperatures. Estimates of daily leaf transpiration rates were obtained by integrating the diurnal curves for each species. Hydrostatic pressures in the tissue apoplasm were measured with a PMS Inst. Co. model 600 pressure chamber fitted with a 0–3-MPa, 150-mm-diameter gauge. The hydrostatic pressures in the tissue apoplasm were assumed to equal the water potentials in the tissue symplasm (Koide et al., 1989). Measurements were made on the terminal 130 mm of recently mature leaves of *A. sandwicense* and on terminal shoots of *D. menziesii*.

in leaf capacitance (Robichaux & Morse, 1990).

The midday temperatures of recently mature leaves of *A. sandwicense* and *D. menziesii* in July do not differ significantly (Table 3). Both species exhibit leaf temperatures of 17–20°C, which is quite moderate given that midday solar irradiances at the study site in July typically exceed 1,020 W m^{-2}, while midday substrate temperatures exceed 55°C. Thus, recently mature leaves of *A. sandwicense* and *D. menziesii* appear to be equally effective at decreasing heat energy inputs and increasing heat energy outputs. In *A. sandwicense*, steep leaf angles and low leaf absorptances (Figs. 3, 5) may aid in decreasing inputs, while high leaf transpiration rates (Table 3) may aid in increasing outputs. In *D. menziesii*, steep leaf angles (Fig. 4) may aid in decreasing inputs, while small leaf sizes (Fig. 5) may aid in increasing outputs.

In marked contrast to recently mature leaves, young leaves of *A. sandwicense* experience very high temperatures for a significant portion of the day (Fig. 7). The young leaves are located at the bottom of the cone-shaped depression in the center of the rosette. During the early morning, when the young leaves are shaded from direct solar irradiance, their temperatures are lower than those of the exposed, recently mature leaves. Once direct solar irradiance penetrates the cone-shaped depression, however, the young leaves experience a rapid increase in temperature and reach maximal temperatures in excess of 37°C by early afternoon. In *D. menziesii*, which lacks the rosette growth form, midday temperatures of young and recently mature leaves are not significantly different.

Argyroxiphium sandwicense and *D. menziesii* thus illustrate the contrasting modes of morphological and physiological adaptation that have evolved within the silversword alliance. Though the

two species grow in the same habitat, they exhibit different suites of traits enabling them to cope with the severe environmental conditions.

Adaptive Radiation

The ecological, morphological, and physiological diversity of species in the silversword alliance is exceptional. The patterns of diversity and genomic relationships among the species suggest that a variety of factors may have played important roles in their adaptive radiation.

First, the periodic origin of new islands in the archipelago may have offered repeated opportunities for interisland dispersal and colonization. At least fourteen major dispersal and colonization events appear to have occurred during the evolutionary history of the silversword alliance (Carr et al., 1989). Founder effects associated with these events may have resulted in the evolution of new morphological and physiological traits.

Second, the wide variety of habitats and wide range of elevations in the archipelago may have facilitated rapid ecological divergence, which is evident in the modern species at grand and local scales. Rapid divergence may have been further enhanced by a genetic system that allowed for a high degree of morphological and physiological flexibility. Striking evidence for such flexibility is provided by *A. sandwicense* and *D. menziesii*, two species that differ radically in morphology and physiology, yet readily produce vigorous, fertile hybrids in nature (Carr & Kyhos, 1981).

Third, chromosomal repatterning at the diploid level may have promoted reproductive isolation between species and may have contributed to the origin of novel gene complexes. Based on cytogenetic evidence, at least eight major genomic arrangements exist among species in the silversword alliance (Carr & Kyhos, 1986; Carr et al., 1989). The genomic arrangements are structurally differentiated via reciprocal chromosome translocation or aneuploid reduction. The degree of postzygotic reproductive isolation between species, as measured by the pollen stainability of hybrids, is strongly correlated with the degree of chromosomal differentiation. With respect to the origin of novel gene complexes, the aneuploid reduction in chromosome number among the *Dubautia* species is correlated with several major ecological, morphological, and physiological differences. Relative to the 14-paired *Dubautia* species, the 13-paired species extend into drier environments, have smaller leaves, and have greater turgor maintenance capacities. Thus, the aneuploid reduction in chromosome number may have been particularly important in the evolutionary history of the silversword alliance.

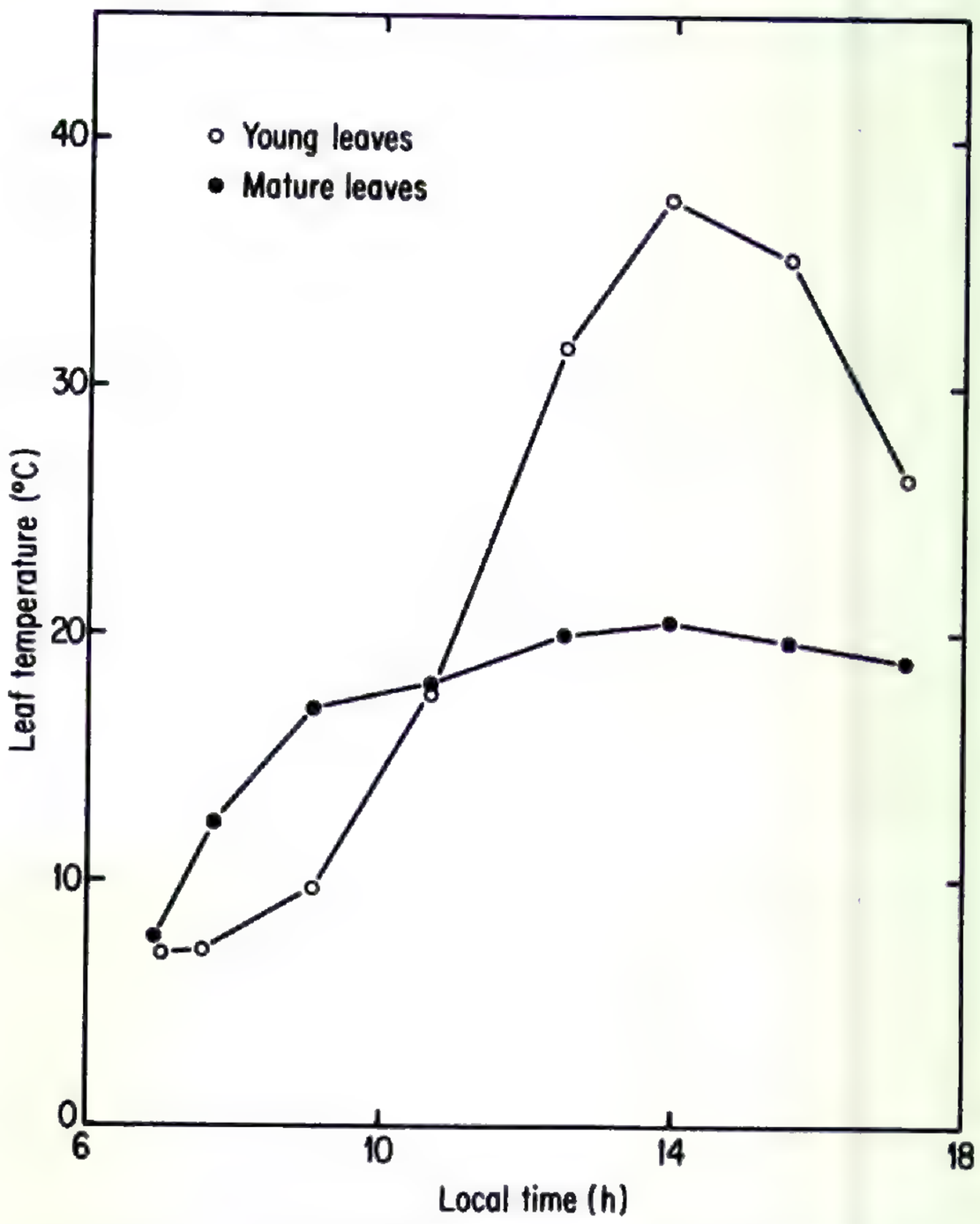

FIGURE 7. Temperatures of young and recently mature leaves of an individual of *Argyroxiphium sandwicense* on 18 July 1982 on Haleakala, Maui. Young leaves were less than 40 mm long. Air temperature was 7.4°C at 0700 hr. and 19.2°C at 1400 hr. Midday solar irradiance exceeded 1,020 W m^{-2}. At 1400 hr. on 2 July 1985, young and recently mature leaves of six individuals of *A. sandwicense* had temperatures of 40.6 ± 0.4°C and 20.2 ± 0.4°C (mean ± 1 S.E.), respectively. The leaf temperatures on 2 July 1985 are significantly different with a *t*-test at $P < 0.001$. The site and measurement techniques were the same as in Table 3.

Understanding the specific roles played by these and other factors in the adaptive radiation of the silversword alliance will require more detailed analyses. Whatever their roles, it is clear that their combined effect has resulted in an extraordinary degree of diversification.

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FLAVONOID DIVERSITY IN RELATION TO SYSTEMATICS AND EVOLUTION OF THE TARWEEDS[1,2]

William J. Crins[3] *and Bruce A. Bohm*[4]

ABSTRACT

The tarweeds produce a diverse array of flavonoids, including glycosylated compounds and methylated aglycones. Extra hydroxylation at positions 6 and/or 8, with frequent O-methylation at these and other positions, is prevalent. This structural diversity coupled with the variety of classes of flavonoids accumulated (flavanones, dihydroflavonols, flavones, flavonols) provides a rich source of characters for study of relationships within and among genera. The distribution of flavonoid aglycones within *Dubautia* is consistent with morphological, cytogenetic, electrophoretic, and phytogeographic evidence bearing on the evolution of its taxa. Flavonoids have also provided a means of assessing the dynamics of hybridization in *Dubautia*. In *Hemizonia*, multivariate analyses of flavonoid arrays have corroborated the view, based on cytogenetic and morphological criteria, that each perennial taxon is independently derived. Ongoing investigations suggest that *Argyroxiphium*, *Calycadenia*, *Holocarpha*, *Layia*, *Wilkesia*, and other genera each exhibit distinctive substitution and accumulation tendencies. Flavonoids may be helpful in developing and testing phylogenetic hypotheses in the Madiinae.

The North American Madiinae (Asteraceae: Heliantheae) consist of about a dozen genera distributed from Baja California to British Columbia, with a major concentration of taxa in California. *Layia* Hook. & Arn. and *Madia* Molina, two of the larger genera, contribute conspicuously to spring floral displays in California. The Hawaiian Madiinae consist of three genera: *Argyroxiphium* DC. with five species, *Dubautia* Gaudich. with 21 species (33 taxa in all), and *Wilkesia* A. Gray with only two species. Arguably the most spectacular members of the island taxa are the subspecies of *A. sandwicense*: subsp. *sandwicense* grows on Mauna Kea on the island of Hawaii; subsp. *macrocephalum* (A. Gray) Meyrat, grows on Haleakala on Maui. Both of these have suffered serious predation and are maintained only with special effort. Species of *Dubautia* occur on all major islands of the archipelago. They exhibit a very wide range of morphological forms and are ecologically the most diverse within the Hawaiian tarweeds. *Wilkesia* consists of two species, *W. gymnoxiphium* A. Gray and *W. hobdyi* H. St. John, both of which are restricted to western Kauai. The former is much more common, occurring in comparatively large populations along the western edge of Waimea Canyon. *Wilkesia hobdyi* is known from only two sites on the far western ends of two ridges and consists of perhaps no more than 200 individuals; it is under severe predation from feral goats and may be on the verge of extirpation.

The Madiinae provide ideal opportunities for the study of evolutionary divergence. In a few genera, hypotheses of species formation have been proposed, and recently tests of these ideas have been conducted using electrophoretic data (Warwick & Gottlieb, 1985; Witter & Carr, 1988). However, it is surprising that in a group as well studied as the tarweeds, so few explicit hypotheses of phylogenetic relationships have been proposed. There now exists a large enough body of data that such hypotheses could be constructed, and these could serve as frameworks for assessment of congruence among different types of data and for testing models of speciation. Flavonoid data could serve in both roles. Since the genetic bases of their biosynthesis are well known (Heller, 1986), these compounds ultimately can be used to construct phylogenies and to assess phylogenies based on other data.

SURVEY AND BIOSYNTHETIC TRENDS

Before dealing with the flavonoids from a phylogenetic viewpoint, we will discuss their structural

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[2] Chemosystematic studies of the tarweeds (Asteraceae: Heliantheae: Madiinae) Number 6.

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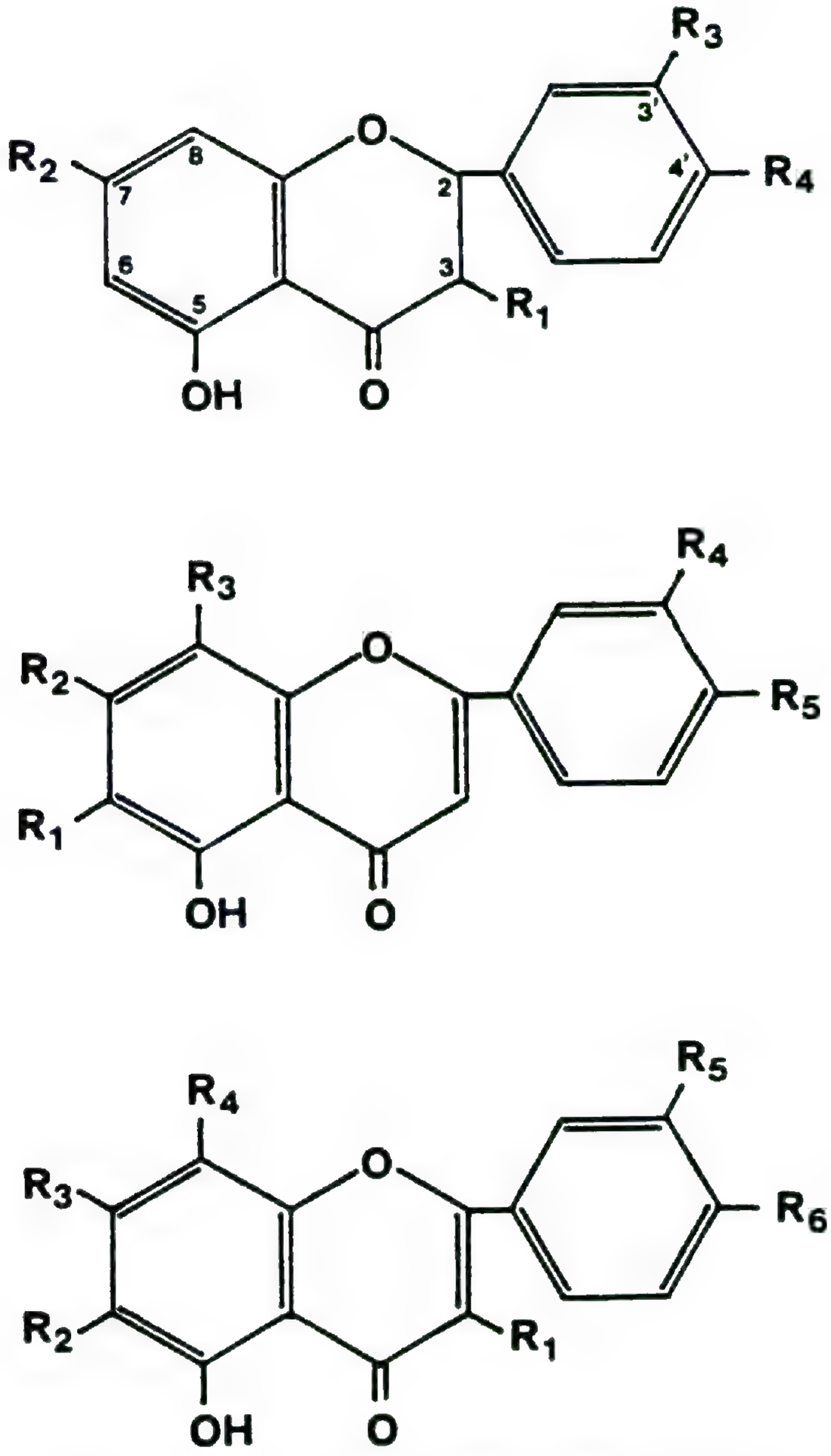


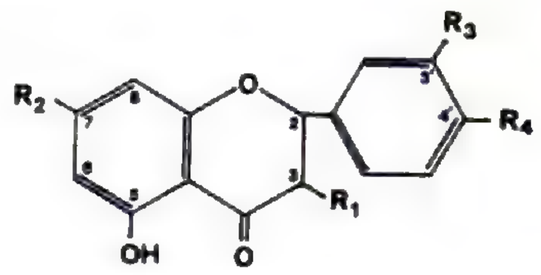
FIGURE 1. Structures of tarweed flavonoid aglycones. Upper structure represents flavanones and dihydroflavonols. Flavones and flavonols are represented by the middle and lower structures, respectively. See Tables 1–3 for substitution patterns (R = H, OH, or OMe) and occurrence of individual compounds in the tarweed genera.

variation and accumulation in the tarweeds. The variety of substitution patterns observed is based upon four flavonoid classes, flavanones, dihydroflavonols, flavones, and flavonols (Fig. 1). The glandular exudates of *Adenothamnus validus* (Brandegee) Keck and all species of *Holocarpha* (DC.) Greene contain all four classes (Crins & Bohm, 1987, 1988a, b). Some of the $n = 13$ (glandular) species of *Dubautia*, such as *D. ciliolata* (DC.) Keck, accumulate flavanones, flavones, and flavonols in their resins, and two classes (flavanones and flavonols) among their vacuolar constituents (Crins et al., 1988a). All species of *Hemizonia* DC. examined so far accumulate flavones and flavonols, and all but one of these also accumulate flavanones (Tanowitz et al., 1987). None of the taxa of *Argyroxiphium*, *Calycadenia* DC., *Lagophylla* Nutt., *Layia*, or *Wilkesia* examined so far accumulate flavanones. Taxa from these genera that do accumulate flavonoids exhibit flavones and flavonols. Two of the species of *Layia* examined, *L. carnosa* (Nutt.) T. & G. and *L. chrysanthemoides* (DC.) A. Gray, lack flavonoids externally, but both secrete large amounts of scopoletin (a coumarin) (Crins et al., 1988b). All tarweeds contain vacuolar glycosylated flavonoids.

Tarweed flavonoids exhibit a wide variety of substitution patterns. Tables 1–3 present the known arrays of flavonoid aglycones in leaf exudates. It is immediately apparent that tarweeds have a propensity for O-methylation. Another prominent feature is the abundance of extra hydroxylation at positions 6 and/or 8, with these hydroxyls frequently being methylated. These series of compounds can be examined in light of biosynthetic considerations, and some generalizations arise. O-Methylation of flavanones can occur at positions 7 and/or 4′. Dihydroflavonols may be formed from their flavanone precursors either before or after O-methylation has occurred. The same is true for later biosynthetic steps (formation of flavones from flavanones or flavonols from dihydroflavonols). However, the series of compounds within a given plant generally suggests that O-methylation at position 7 occurs early in the biosynthetic pathway and that extra hydroxylation occurs after the bond between carbons 2 and 3 has become unsaturated. We have found no evidence of 6-hydroxyflavanones or 6-hydroxydihydroflavonols. [The report of 6-hydroxyeriodictyol 7-methyl ether by Crins & Bohm (1987) must be corrected to 7-O-methyldihydroquercetin in light of new evidence on structural differentiation of flavanones and dihydroflavonols using mass spectrometry (Balza et al., 1988).] The affinities of the 6- (and 8-) O-methyltransferase enzymes for their substrates must be very high, as 6- and 8-hydroxy derivatives are only infrequently encountered.

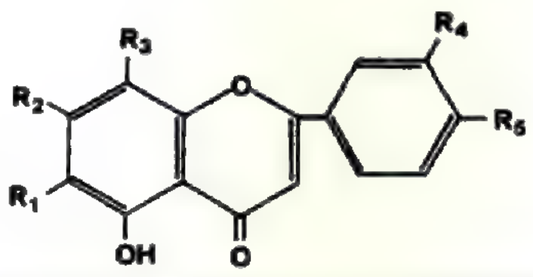
Several taxa lack external flavonoid aglycones. In *Layia chrysanthemoides*, loss of glandular structures is correlated with the inability to secrete these compounds, although the leaf wash did contain the coumarin scopoletin. In the $n = 14$ *Dubautia* taxa, glands are absent from the foliage and stem, although there may be some glands on the pedicels and corollas (Carr, 1985). In most cases insufficient flowering material was available to test for flavonoids. However, in the case of *D. scabra* (DC.) Keck, where large amounts of flowering material was available, flavonoids were not detected (Crins et al., 1988a). In several mainland

TABLE 1. Occurrence and substitution patterns of flavanones and dihydroflavonols in tarweed genera. R-groups on model structure correspond to R-groups in columns one to four. H = hydrogen; OH = hydroxyl group; OMe = methoxyl group; Ad = *Adenothamnus*; D = *Dubautia*; Hm = *Hemizonia*; Ho = *Holocarpha*; M = *Madia*. Data for *Madia* are based on an incomplete survey of *M. elegans* D. Don.



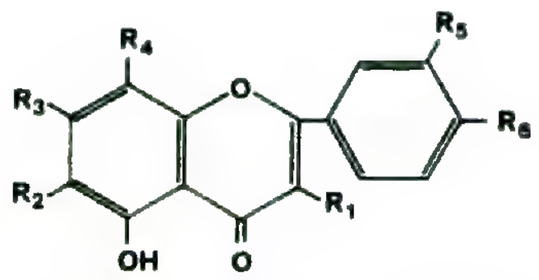
Substitution pattern				Genus				
R_1	R_2	R_3	R_4	Ad	D	Hm	Ho	M
H	OH	H	OH	+	+	+	−	−
H	OH	H	OMe	+	−	−	−	−
H	OMe	H	OH	−	+	−	−	−
H	OMe	H	OMe	+	−	−	+	−
H	OH	OH	OH	−	−	+	−	−
H	OMe	OH	OH	+	+	+	+	−
H	OMe	OH	OMe	+	−	−	−	−
OH	OMe	OH	OH	+	−	−	+	+

TABLE 2. Occurrence and substitution patterns of flavones in the tarweed genera. R-groups on model structure correspond to R-groups in columns one to five. H = hydrogen; OH = hydroxyl; OMe = methoxyl; Ad = *Adenothamnus*; Ar = *Argyroxiphium*; C = *Calycadenia*; D = *Dubautia*; Hm = *Hemizonia*; Ho = *Holocarpha*; Lg = *Lagophylla*; Ly = *Layia*; M = *Madia*; W = *Wilkesia*.



Substitution pattern					Genus									
R_1	R_2	R_3	R_4	R_5	Ad	Ar	C	D	Hm	Ho	Lg	Ly	M	W
H	OH	H	H	OH	−	+	−	+	−	+	−	+	+	−
H	OMe	H	H	OH	−	−	−	+	−	−	+	−	−	−
OH	OH	H	H	OH	−	−	−	+	−	−	−	−	−	−
OMe	OH	H	H	OH	+	−	−	+	−	−	−	+	+	−
OMe	OMe	H	H	OH	−	+	−	+	−	−	+	+	−	+
OMe	OH	H	H	OMe	−	−	−	−	−	−	−	+	−	−
H	OH	OMe	H	OH	−	−	−	+	−	−	−	−	+	+
H	OMe	OMe	H	OH	−	+	−	−	−	−	−	−	−	+
OMe	OH	OMe	H	OH	−	−	−	−	−	−	−	−	−	+
OMe	OMe	OMe	H	OH	−	+	−	−	−	−	−	−	−	+
H	OH	H	OH	OH	−	−	−	−	+	−	−	−	−	−
H	OMe	H	OH	OH	+	−	−	+	−	+	−	−	−	+
H	OH	H	OH	OMe	−	−	−	+	−	−	−	−	−	−
H	OH	OMe	OH	OH	−	−	−	−	−	−	−	−	−	+
OMe	OH	H	OH	OH	+	−	−	−	−	−	−	+	−	−
OMe	OH	H	OMe	OH	−	−	−	−	−	+	+	−	−	−
OMe	OH	H	OMe	OMe	−	−	−	−	−	−	−	+	−	−
OMe	OMe	H	OH	OH	−	−	−	+	−	−	−	−	−	+
OMe	OMe	H	OMe	OMe	−	−	−	−	−	−	+	−	−	−
OMe	OH	OH	OH	OH	−	−	−	−	+	−	−	−	−	−
OMe	OH	OMe	OH	OH	−	−	−	−	−	−	−	−	−	+
OMe	OMe	OMe	OH	OH	−	−	−	−	−	−	−	−	−	+
OMe	OMe	OMe	OMe	OH	−	−	+	−	−	−	−	−	−	−

TABLE 3. Occurrence and substitution patterns of flavonols in tarweed genera. R-groups on model structure correspond to R-groups in columns one to six. H = hydrogen; OH = hydroxyl; OMe = methoxyl; Ad = *Adenothamnus*; Ar = *Argyroxiphium*; C = *Calycadenia*; D = *Dubautia*; Hm = *Hemizonia*; Ho = *Holocarpha*; Lg = *Lagophylla*; Ly = *Layia*; M = *Madia*; W = *Wilkesia*.



Substitution pattern						Genus									
R_1	R_2	R_3	R_4	R_5	R_6	Ad	Ar	C	D	Hm	Ho	Lg	Ly	M	W
OH	H	OH	H	H	OH	−	−	−	+	−	−	−	−	−	−
OMe	H	OH	H	H	OH	+	−	−	−	−	+	−	−	−	+
OH	H	OMe	H	H	OH	−	−	−	+	−	+	−	−	−	−
OH	H	OH	H	H	OMe	−	−	−	−	+	−	−	−	−	−
OMe	OMe	OH	H	H	OH	+	−	+	−	−	−	−	+	−	−
OMe	OMe	OMe	OMe	H	OH	−	−	+	−	−	−	−	−	−	−
OH	H	OH	H	OH	OH	−	−	−	+	+	−	−	−	−	−
OMe	H	OH	H	OH	OH	−	−	−	−	+	+	−	−	+	−
OMe	H	OH	H	OMe	OH	−	−	−	−	−	+	−	−	+	−
OH	H	OMe	H	OH	OH	+	−	−	−	−	+	−	−	−	−
OMe	H	OMe	H	OH	OH	−	−	−	−	+	+	−	−	−	−
OMe	OH	OMe	H	OH	OH	−	−	−	−	−	+	−	−	−	−
OH	OMe	OH	H	OH	OH	−	−	−	−	+	−	−	−	−	−
OMe	OMe	OH	H	OH	OH	−	−	−	−	+	+	−	−	−	−
OMe	OMe	OH	H	OMe	OH	−	−	−	−	−	−	+	−	−	−
OMe	OMe	OMe	H	OH	OH	−	−	−	−	+	−	+	−	−	−
OMe	OMe	OMe	H	OH	OMe	−	−	−	−	−	−	+	−	−	−
OMe	OH	OMe	OMe	OH	OH	−	−	+	−	−	−	−	−	−	−
OMe	OMe	OH	OMe	OH	OH	−	−	−	−	+	−	−	−	−	−
OMe	OMe	OMe	OMe	OH	OH	−	−	+	−	−	−	−	−	+	+
OMe	OMe	OMe	OMe	OMe	OH	−	−	+	−	−	−	−	−	−	−
OMe	H	OH	OMe	OH	OH	−	−	−	−	+	−	−	−	−	−
OMe	H	OMe	OMe	OH	OH	−	−	+	−	+	−	−	−	−	−

tarweeds, glands are present but no flavonoid aglycones are secreted: *Achyrachaena mollis* Schauer, *Blepharipappus scaber* Hook., *Lagophylla minor* (Keck) Keck, *L. ramosissima* Nutt., and *Layia carnosa*. Coumarins were observed in some of these, however (Crins et al., 1988b). Many of these plants have highly reduced or modified floral and/or inflorescence structures compared with their congeners, or the subtribe as a whole. *Achyrachaena mollis* is clearly divergent, with its reduced, yellow-orange rays and reduced inflorescence. Within *Lagophylla*, *L. minor* has few glands, and *L. ramosissima* has greatly reduced capitula, compared with such species as *L. glandulosa* A. Gray, which yields copious flavonoid-rich resin. *Layia carnosa* is clearly differentiated from other *Layia* species by its reduced white rays and specialized habitat preference.

Some trends are beginning to emerge in terms of accumulation tendencies and substitution patterns among the ten genera for which we have data. *Adenothamnus validus*, *Hemizonia* species, and *Holocarpha* species accumulate flavanones, as do several xerophytic species of *Dubautia*: *D. arborea* (A. Gray) Keck, *D. ciliolata*, and *D. linearis* (Gaudich.) Keck subsp. *hillebrandii* (H. Mann) G. Carr. These three taxa of *Dubautia* occur on the island of Hawaii. In contrast, *D. linearis* subsp. *linearis* from Lanai, and *D. sherffiana* Fosb. from Oahu (both $n = 13$) have much less diverse arrays of external flavonoids, and they do not accumulate flavanones. This trend is further emphasized since all $n = 14$ taxa lack external flavonoids and they all occur on the older islands. Thus, flavonoid diversity parallels cytological and morphological radiation in *Dubautia* (Carr, 1985; Crins et al., 1988a; Crins & Bohm, unpublished data).

The capacity of a particular taxon to accumulate flavanones and dihydroflavonols must be used judiciously in considering relationships since these classes of compound serve as precursors of flavones and flavonols, respectively (Heller, 1986). However, if flavanones or dihydroflavonols exhibit substitution patterns that are not seen in flavones or

flavonols from the same taxon, then information of phylogenetic interest can be gained. Methylation at any hydroxylated position on the flavonoid nucleus requires a specific O-methyltransferase; a high level of site selectivity has also been shown for O-glycosyltransferases (Heller, 1986; Ibrahim et al., 1987). Assuming that such enzyme specificity is general in plants, relationships of taxa within genera and perhaps among genera in the Madiinae can be examined.

In *Adenothamnus* and *Holocarpha*, one flavanone (7,4′-dimethylnaringenin), present in large quantities, has no counterpart among suites of flavones and flavonols. Thus it appears that the 4′-O-methylation step is unrelated to subsequent biosynthetic steps, and this flavanone is an accumulation product in its own right. This is also true of 4′-methylnaringenin and persicogenin in *Adenothamnus*.

On the generic level some common tendencies in substitution patterns are apparent among flavones and flavonols. *Argyroxiphium* appears to produce only flavones, but only one species has been examined. Four genera have 3-unsubstituted flavonols in their pigment profiles, *Adenothamnus*, *Dubautia*, *Hemizonia*, and *Holocarpha*. Of this group only *Dubautia* lacks the corresponding 3-O-methyl derivatives. All genera are capable of 7-O-methylation although each genus also contains compounds in which the 7-hydroxyl group remains unsubstituted. All genera produce at least one 6-O-methylated compound. Less common is 8-O-methylation, which was observed in *Argyroxiphium*, *Calycadenia*, *Dubautia*, *Hemizonia*, *Madia*, and *Wilkesia*. Within the Madiinae as a whole there is a strong tendency for the hydroxyl groups at positions 6 and/or 8 to be methylated. Only three of ten genera studied exhibit 6-hydroxyflavonoids (*Calycadenia*, *Dubautia*, and *Holocarpha*), and only *Hemizonia* contains 8-hydroxyflavonoids. B-Ring O-methylation of flavones and flavonols is also restricted in distribution: 3′-O-methylation is seen in *Calycadenia*, *Holocarpha*, *Lagophylla*, *Layia*, and *Madia*, and 4′-O-methylation is known only in *Dubautia*, *Hemizonia*, *Lagophylla*, and *Layia*. *Lagophylla glandulosa* and *Layia hieracioides* (DC.) Hook. & Arn. are alone in exhibiting 3′,4′-di-O-methylation (Crins et al., 1988b).

Evolutionary Trends

Analysis of Hybrids in *Dubautia*

We begin our discussion of the application of flavonoid data to tarweed systematics by examining a case of natural hybridization between two species of *Dubautia*. On the island of Hawaii, lava flows from two of its major volcanoes, Mauna Loa and Mauna Kea, meet in an area known as the "Saddle." *Dubautia scabra* ($n = 14$) and *D. ciliolata* ($n = 13$) co-occur here. *Dubautia scabra* exhibits very high chromosomal homology with all of the $n = 13$ species and is considered to be their nearest living ancestor (Carr, 1985). Natural hybrids have developed in areas of marginal or intermediate habitat in the contact zone. Carr & Kyhos (1981) suggested that these hybrids were generally F_1s with a few higher-generation recombinants perhaps also present.

Flavonoid data clarify the nature of the hybrid population. The flavonoid glycosides of the parental species differ, with *D. ciliolata* producing kaempferol and quercetin 3-O-monoglucosides and 3-O-rhamnosylgalactosides and *D. scabra* producing quercetin 3-O-glucoside and 6-O-methoxyflavonol mono- and diglycosides. The hybrids share 3-O-monoglucosides with both parents, but all of their diglycosides are "hybrid" compounds, with rhamnose being derived from *D. ciliolata* and glucose from *D. scabra* (Crins et al., 1988a). All of the hybrid plants contain the same array of glycosides.

Glandular resins allow further resolution of the structure of the hybrid population. *Dubautia scabra* does not produce external flavonoids; the resin of *D. ciliolata* contains several flavones, two flavanones, and one flavonol. Quercetin and kaempferol appear to be restricted to the hybrids possibly on account of recombination or other disruption of biosynthesis.

The varying distributions of compounds among hybrid plants indicate differing degrees of disruption of biosynthetic pathways, which suggests the presence of higher-generation recombinants. When considering the entire set of hybrids in the sample, gradation in the complexity of flavonoid aglycone arrays emerges. The field-collected hybrids show considerable variation in their arrays. However, synthetic F_1 hybrids produced under controlled conditions were chemically uniform. Comparison of the flavonoid chemistry of the synthetic and natural hybrids strongly suggests that all of the natural hybrids are at least second-generation crosses, and the complexities of some of their profiles suggests introgression toward *D. ciliolata*.

Population Analysis in *Calycadenia*

Resin flavonoids have also served usefully as markers of inter- and intrapopulational differences in *Calycadenia ciliosa* Greene (Emerson et al., 1986). *Calycadenia ciliosa* consists of at least five structurally distinct chromosome races (Carr &

Carr, 1983), and high degrees of structural heterozygosity in some populations complicate the situation. The Dry Creek race is the most variable morphologically, the most widespread geographically (Carr & Carr, 1983), and the most diverse chemically (Emerson et al., 1986). In fact, there is a striking correlation among morphological variability, geographical extent, and chemical diversity in all races of *C. ciliosa*. For the most part, flavonoid data concur with the cytogenetic results. However, it seems that the Dry Creek race is most likely to be the primitive race, rather than Ciliosa, as concluded earlier (Emerson et al., 1986), since the former has the most complex array of flavonoids, including the only compound with a monohydroxylated B-ring. The Lewiston and Corning races both accumulate 5,3′,4′-trihydroxy-3,6,7,8-tetramethoxyflavone along with one of its precursors unsubstituted at position 8. None of the precursors remain in the Ciliosa and Pillsbury races, suggesting increased efficiency in substrate utilization.

FLAVONOID PATTERNS WITHIN *DUBAUTIA*

Several interesting evolutionary problems can be found in the genus *Dubautia*, whose 21 species (33 taxa in all) are ordered into three sections. Section *Dubautia* consists of ten species (18 taxa) and is characterized by having $n = 14$ and, relevant to our interests, being eglandular and thus lacking resinous flavonoids. Section *Venoso-reticulatae* (A. Gray) G. Carr consists of only *D. latifolia* (A. Gray) Keck which has $n = 14$, is eglandular, and, interestingly, is a liana. The remaining ten species (14 taxa) comprise sect. *Railliardia*, which is heterogeneous with regard to chromosome number and leaf surface chemistry. All taxa in this last section have $n = 13$ except *D. scabra*, which has $n = 14$ in common with the other two sections. It also lacks leaf surface flavonoids in common with the other two sections. *Dubautia scabra* is considered to be the nearest extant relative to the $n = 13$ species, as indicated by enzyme electrophoretic data (Witter & Carr, 1988). The absence of flavonoid aglycones in *Dubautia herbstobatae* is more difficult to explain. It may have resulted from a reversal to a nonglandular state, or this may be a more primitive taxon than has previously been suspected. *Dubautia herbstobatae* might have been the first offshoot of the $n = 13$ lineage, before glandularity and flavonoid secretion became prominent features of the group, a contention supported by its occurrence on Oahu, the oldest island, on which $n = 13$ species presently occur (Fig. 2).

Within the $n = 13$ glandular species it is possible to distinguish two groups based on comparative complexity of flavonoid profiles. *Dubautia linearis* subsp. *linearis*, *D. reticulata* (Sherff) Keck, and *D. sherffiana* have simple aglycone profiles consisting of three compounds each. A close relationship between *D. linearis* subsp. *linearis* and *D. sherffiana* is suggested by their identical profiles. This is the only case in *Dubautia* where profiles of two different taxa were identical. The other three species in the $n = 13$ glandular group that we have examined, *D. arborea*, *D. ciliolata* subsp. *glutinosa* G. Carr, and *D. linearis* subsp. *hillebrandii*, exhibit much more complex arrays of flavonoids in their resins. Each of these latter three taxa has its own peculiar profile. One of the more interesting things to emerge from flavonoid analysis of this group of taxa is the dissimilarity between these two subspecies of *D. linearis*. *Dubautia linearis* subsp. *linearis* occurs on Maui and Lanai (but not on Hawaii), while *D. linearis* subsp. *hillebrandii* occurs on the island of Hawaii. (*Dubautia linearis* subsp. *opposita* (Sherff) G. Carr) occurs on Molokai and was not available for study.) *Dubautia linearis* subsp. *linearis* has a flavonoid pattern identical to that of *D. sherffiana*. This relationship is supported by close similarities in vegetative anatomy (Carlquist, 1959) and morphology (Carr, 1985). *Dubautia linearis* subsp. *hillebrandii* differs substantially from subsp. *linearis* and may be more closely related to other taxa from the islands of Maui and Hawaii, contrary to its current placement in *D. linearis*. In fact, Carlquist (1959) pointed out the anatomical and morphological similarities of subsp. *hillebrandii* with *D. arborea* and *D. menziesii* (A. Gray) Keck. Furthermore, Witter & Carr (1988) showed that subsp. *hillebrandii* had higher genetic identities with *D. reticulata*, *D. dolosa* (Degener & Sherff) G. Carr, *D. platyphylla* (A. Gray) Keck, *D. menziesii*, and *D. arborea* than it did with *D. sherffiana*. (Data for *D. linearis* subsp. *linearis* were not available for comparison.) Further studies of this system will be necessary to gain a better understanding of relationships.

Flavonoid glycoside patterns may likewise provide indications of relationships within *Dubautia*. On a relatively coarse scale, the presence of an eriodictyol glycoside correlates well with the xerophytic habit, although at least two mesophytes (*D. laxa* Hook. & Arn. subsp. *hirsuta* (Hillebrand) G. Carr and *D. microcephala* Skottsb.) also contain this compound. On the other hand, several of the mesophytes (*D. knudsenii* Hillebrand subsp. *knudsenii*, *D. laevigata* A. Gray, *D. latifolia* (A. Gray)

Keck, *D. plantaginea* Gaudich. subsp. *plantaginea*, and *D. raillardioides* Hillebrand) lack this compound. It is unclear whether the occurrence of this compound signifies relationship, or whether this is a case of parallelism (see discussions of *Hemizonia* and *Holocarpha* below), since the suggested relationships of these mesophytes to the xerophytes do not conform to those presented in the scheme of Witter & Carr (1988).

MULTIVARIATE ANALYSIS OF *HEMIZONIA* FLAVONOIDS

Tanowitz and associates (Proksch et al., 1984; Tanowitz et al., 1987) have examined the flavonoid aglycones of several species of *Hemizonia*. In their work we can also look for indications of relationships at the macroevolutionary level. They attempted to elucidate relationships by comparing the flavonoid aglycone arrays of 18 taxa of *Hemizonia*, including three perennials (*H. greeneana* Palmer subsp. *peninsularis* Moran, *H. minthornii* Jepson, and *H. streetsii* A. Gray) using phenetic methods. Their ordination and clustering results suggest that each of these taxa belongs to a different subgroup within a heterogeneous assemblage of taxa, including *H. fitchii* A. Gray of sect. *Centromadia* Keck, and an assortment of species from sect. *Madiomeris* Nutt as emended by Tanowitz. The cluster analysis also split sect. *Madiomeris* into two groups.

If we consider the phenetic relationships within sect. *Madiomeris* in a flavonoid biosynthetic context, several contrasts are evident. Before proceeding it is important to remember that the presence of a compound in a profile requires that all precursors in its pathway must have been present at some time so that, although the absence of a compound will affect the computation of distance measures, it will not necessarily affect an estimate of relationship based on biosynthetic principles.

After recoding the data to account for precursors (only unique end products are useful for phylogenetic analysis) there are only six compounds that can potentially yield useful phylogenetic information and one additional compound that serves as an autapomorphy. When this data set is analyzed using Penny's branch-and-bound method to determine the most parsimonious trees (using PHYLIP), two topologies are found. (Since a few taxa from this section are not included in the data set owing to lack of flavonoid data, the group analyzed is paraphyletic.) Nevertheless, the topologies provide novel frameworks for testing ideas about relationships within the section. Figure 3 illustrates the topologies and a consensus tree based on them.

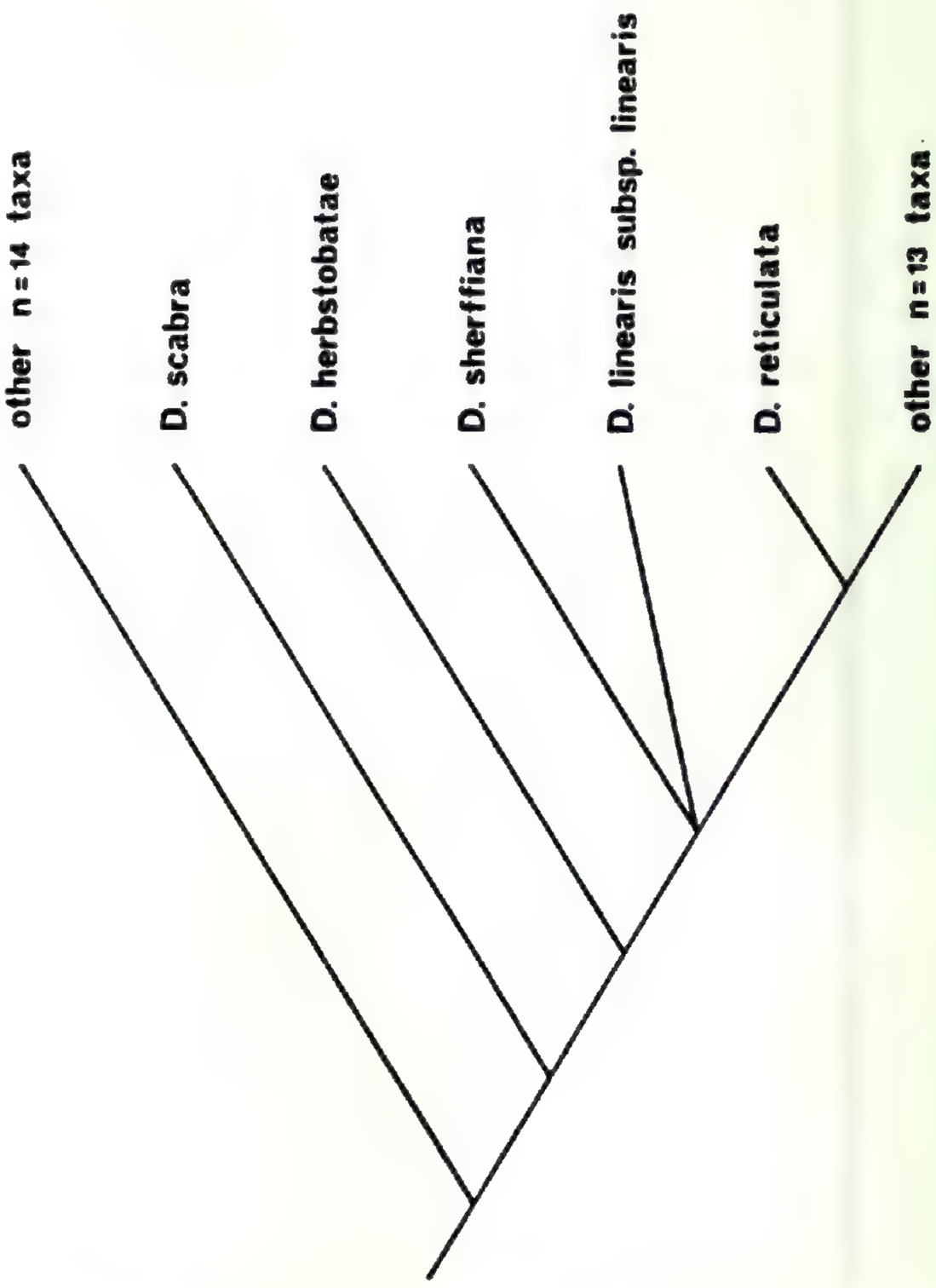


FIGURE 2. Partial resolution of phylogenetic relationships within *Dubautia* sect. *Railliardia*, based on flavonoid aglycones.

Although the consensus tree is very poorly resolved, it suggests that two subgroups exist within sect. *Madiomeris* (excluding the perennials). These subgroups are not entirely consistent with the groupings found in the phenetic analyses reported by Tanowitz et al. (1987). In their group II, *H. halliana* Keck is included with *H. arida* Keck, *H. fasciculata* (DC.) T. & G., *H. pallida* Keck, and *H. paniculata*. *Hemizonia pentactis* (Keck) Keck is placed in their group III. The group placements of *H. halliana* and *H. pentactis* are reversed in our analysis relative to their positions in the phenetic analysis of Tanowitz et al. (1987).

When the data for the three perennials are included in the analysis, almost 1,500 most parsimonious trees are possible. It has not been possible to examine more than a small number of these trees, but a few features are worthy of note. In the sample of 50 trees examined, *H. arida*, *H. fasciculata*, *H. pallida*, *H. paniculata*, and *H. pentactis* are always maintained as a group. However, the distinction between these five taxa and the other group found when perennials were excluded (consensus tree, Fig. 3) is not always upheld. Little can be said about the relationships of the perennials, except that *H. streetsii* is always grouped with *H. lobbii* in the 50 trees. Thus, the flavonoid

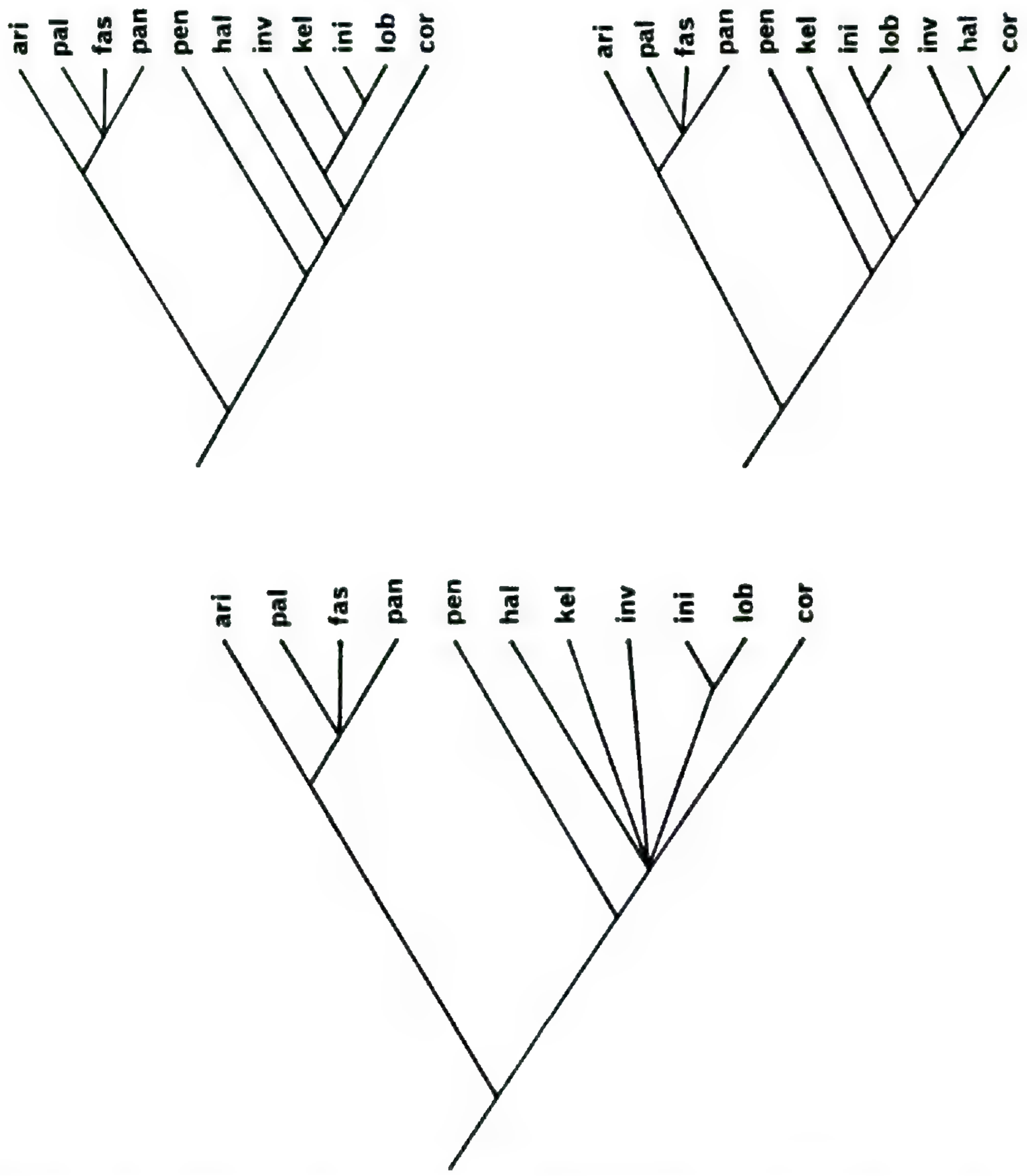


FIGURE 3. Alternative phylogenetic trees of the taxa of *Hemizonia* sect. *Madiomeris* for which flavonoid aglycone data are available, and their consensus tree. Key to species names: Ari = *H. arida*; Con = *H. conjugens*; Cor = *H. corymbosa*; Fas = *H. fasciculata*; Hal = *H. halliana*; Inc = *H. increscens*; Kel = *H. kelloggii*; Lob = *H. lobbii*; Pal = *H. pallida*; Pan = *H. paniculata*; Pen = *H. pentactis*.

data provide general indications of relationship within sect. *Madiomeris*, but fine-scale resolution does not seem possible.

PHYLOGENETIC ANALYSIS OF *HOLOCARPHA* USING FLAVONOIDS

Whenever possible, an attempt should be made to integrate all available information into a classification scheme or a phylogenetic hypothesis. In a sense, this has been done with *Hemizonia*, where a recently revised genus has been studied in terms of its flavonoid chemistry, and further suggestions about relationships have been set forth. However, data are incomplete for many taxa, and no explicit phylogeny for the genus has been proposed against which the chemical data could be examined. Since there is no consensus about the way in which chemical changes occur during the process of evolution (Gornall & Bohm, 1978), a test of congruence of chemical data against a phylogeny derived from other sources (morphology, cytology, etc.) would be more prudent. In the case of *Holocarpha*, a genus of four summer-flowering, self-incompatible annuals, we generated several alternative cladograms using various algorithms (PHYLIP version 2.8, Felsenstein, 1985). Three cladograms were based on 12 discrete-state morphological characters, one 'cladogram' was based on a scenario where two independent aneuploid events were hypothesized. The most parsimonious cladogram for the morphological data set was supported by four different algorithms (Crins & Bohm, 1988b). Flavonoid aglycone biosynthetic data were then superimposed on these topologies.

Fourteen compounds have been characterized from species of *Holocarpha*. The presence or absence of terminal steps in the biosynthetic network are more or less species-specific. For example, the capacity to hydroxylate position 6 in 3,7-di-O-methylquercetin is lost in *H. macradenia* (DC.) Greene, and only *H. heermannii* (Greene) Keck can dehydrogenate the 2-3 bond and subsequently methylate the hydroxyl group at carbon-3.

The three cladograms yield similar results in terms of their congruence with the flavonoid data. All three require parallel losses of the capacity to produce 7-O-methylluteolin in *H. heermannii* and *H. macradenia*, and 3-O-methylquercetin and 3,3′-di-O-methylquercetin in *H. obconica* (Clausen & Keck) Keck and *H. macradenia*. All other losses or gains in biosynthetic capacity are autapomorphies. The least parsimonious tree for morphological characters requires only a single parallelism, for the loss of 7-O-methylluteolin. The loss of methylated quercetin derivatives is a synapomorphy uniting *H. macradenia* and *H. obconica* on this tree. The tree most consistent with the chemical data is the least parsimonious on morphological and cytological grounds (Crins & Bohm, 1988b). It should be noted that the difference (based on flavonoid data) is a single step, however. In the present case, where morphological, cytological, and ecological (Palmer, 1982) data all support a parsimonious hypothesis of evolution, we must suggest that flavonoid aglycone biosynthesis has undergone some degree of parallelism in terms of losses in different lineages. We cannot ignore the bulk of evidence in favor of a more parsimonious interpretation of chemical changes.

SOME OBSERVATIONS ON *LAYIA*

In *Layia*, Clausen et al. (1941) defined several species on morphological and cytological grounds. Its 15 species are considered to have diverged through specialization of peripheral populations on novel substrates or in new habitats (geographical speciation). Warwick & Gottlieb (1985) obtained evidence from enzyme electrophoretic studies that supported the geographical speciation hypothesis for the species with $n = 7$. Flavonoid aglycones have also provided some support for this hypothesis. The identical nonpolar phenolic profile of *L. platyglossa* (F. & M.) A. Gray ($n = 7$) and *L. glandulosa* (Hook.) Hook. & Arn. ($n = 8$) suggests that they are close relatives, as did the hybridization experiments of Clausen et al. (1941). This evidence suggests aneuploidy with little subsequent differentiation in the genome.

Although more taxa must be examined, a pattern is emerging in which flavonoid aglycone diversity increases from total absence in *L. chrysanthemoides* ($n = 7$) to the profiles of *L. glandulosa* and *L. platyglossa* ($n = 7$), which contain a small number of compounds, to the richer profiles of the *L. hieracioides* ($n = 8$)–*L. paniculata* Keck ($n = 16$) group. *Layia septentrionalis* Keck ($n = 8$) is an outlier in that it lacks the flavonol aglycone biosynthetic pathway, and *L. carnosa* ($n = 8$) is also an outlier, lacking flavonoid aglycones entirely. It seems that as each derivative species arose, independent chemical changes occurred. There is an overall trend toward increasing complexity in the flavonoid aglycone composition of the resin, assuming that $n = 7$ is the basic chromosome number of the genus (Gottlieb, 1987), but individual offshoots (*L. paniculata*, *L. septentrionalis*, *L. carnosa*) have taken different, occasionally divergent, routes in the process. As more species are examined, the flavonoid data should facilitate our understanding of the phylogenetic history of the genus.

FUTURE DIRECTIONS

Studies of flavonoid occurrence and variation within the tarweeds have begun to provide new insights into the modes and directions of evolution in this diverse group. Some of the numerous problems requiring attention have been mentioned above. Phylogenetic hypotheses, especially for the larger genera such as *Calycadenia*, *Hemizonia*, and *Madia* can serve as templates for the assessment of congruence with chemical and other data sets. There are numerous taxa in these and other genera for which no flavonoid or other chemical data are available. Table 4 summarizes the current state of the flavonoid surveys. We have concentrated largely on flavonoid aglycones, but our examination of flavonoid glycosides in two species of *Dubautia* and their natural hybrids indicates that these polar compounds will also be useful in tracking microevolution (Crins et al., 1988a). Preliminary chromatographic examinations of glycosides in a wide range of tarweed taxa reveal substantial differences in the occurrence of compounds that may be useful in macroevolutionary studies. These sorts of analyses provide a feedback mechanism whereby we learn more about the scale at which different types of data are useful in tracking evolution. In some cases, flavonoid suites suggest that biosynthetic parallelisms have occurred (e.g., *Hemizonia* and *Holocarpha*); in other cases, losses or gains in biosynthetic capability appear to be species-specific (e.g., *Holocarpha* and *Layia*); and in still others, flavonoids serve as accurate markers of population differentiation (e.g., *Calycadenia*).

Little is known of the functional significance of flavonoids in tarweeds or in most other groups of plants. Because of the rich and variable arrays of compounds produced by different species of tarweeds, these plants may be useful for studying flavonoids as ultraviolet radiation shields, as anti-

TABLE 4. Summary of progress in tarweed flavonoid survey. 2D TLC = chromatographic evidence for flavonoid glycosides. +/− = some species produce exudate flavonoids, some do not. The "?" indicates that no data exist at the moment.

Genera	Total numbers of species	Numbers of species examined	Flavonoid glycosides	Flavonoid aglycones	Sources of data
Achyrachaena	1	1	+ (2D TLC)	none	Crins & Bohm (unpublished data)
Adenothamnus	1	1	+	+	Crins & Bohm (1988a)
Argyroxiphium	5	2	+	+	Bohm & Fong (unpublished data)
Blepharippapus	1	1	+ (2D TLC)	none	Crins & Bohm (unpublished data)
Blepharizonia	1	0	?	?	
Calycadenia	11	5	+	+	Emerson et al. (1986)
Dubautia	21	18	+	+/−	Crins et al. (1988a)
Hemizonia	32	17	?	+	Proksch et al. (1984); Tanowitz et al. (1987)
Holocarpha	4	4	?	+	Crins & Bohm (1987); Crins & Bohm (unpublished data)
Holozonia	1	0	?	?	
Lagophylla	5	3	?	+/−	Crins & Bohm (unpublished data)
Layia	15	7	+ (2D TLC)	+/−	Crins et al. (1988b)
Madia	20	8	?	+	Bohm et al. (unpublished data)
Raillardella	5	1	+ (2D TLC)	none	Crins & Bohm (unpublished data)
Wilkesia	2	2	?	+	Bohm & Fong (unpublished data)

herbivore defense compounds, or as factors in the floral biology of the tarweeds. For example, *Dubautia* contains species in virtually all of the available habitats in the Hawaiian Islands, and flavonoid aglycone diversity is correlated with habitat as well as the age of individual islands. This system might provide an excellent opportunity to examine the relative requirements for UV screening, with species in mesic habitats presumably requiring far less protection than species in xeric environments. The relative effectiveness of different flavonoids in UV screening is unknown.

Experiments addressing the question of why such diverse arrays of compounds are produced by some species are also needed. Any study of coevolution that attempts to incorporate the role of flavonoids will require knowledge of the organisms with which the tarweeds interact. Flavonoids (at least aglycones) probably contribute to antiherbivore defenses, just as other secreted natural products, such as benzofurans and chromenes, do (Proksch & Rodriguez, 1983), but no conclusive experimental evidence is available. There is also a lack of data about natural herbivores, parasites, and pathogens of tarweeds.

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BIODIVERSITY AND CYTOGENETICS OF THE TARWEEDS (ASTERACEAE: HELIANTHEAE–MADIINAE)[1]

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ABSTRACT

Because the tarweeds (Madiinae) attracted the attention of early pioneers in the areas of genecology and biosystematics, this assemblage of plants has been studied more intensively than most comparably sized groups. The tarweeds comprise 127 species in 17 genera, with centers of diversity in California and Hawaii. The biological diversity of the tarweeds is extreme. The Hawaiian members alone include herbaceous mat-forming plants, cushion plants, monocarpic and polycarpic shrubs, trees, and lianas. Collectively, the group includes self-compatible and self-incompatible annuals and perennials. An extremely conspicuous component of the diversification of tarweeds has been chromosome evolution such that gametic numbers of $n = 4–14$, 16, 17, 24, and 34 are represented by one or more taxa. An analysis of this variation suggests that the ancestral chromosome number in the Madiinae is $n = 7$. The numerous infrageneric and nine intergeneric hybrid combinations known in the Madiinae are summarized. Among the latter hybrids, one indicates a close relationship between *Raillardiopsis muirii* and *Madia bolanderi*, and another establishes a genetic link between the mainland and Hawaiian representatives of the group.

The tarweed subtribe (Madiinae) of the sunflower tribe Heliantheae has been subjected to intensive biosystematic investigations for over 75 years. The tarweeds first captured the attention of the innovative experimental systematist H. M. Hall in 1912. In 1915, Hall enlisted the efforts of E. B. Babcock in a comprehensive treatment of the hay-field tarweeds (Babcock & Hall, 1924). The early tarweed studies were carried out at the University of California, but Hall joined the Carnegie Institution of Washington in 1919, and the center of tarweed research eventually shifted to Stanford. Before his death, Hall was able to welcome Jens Clausen to the growing staff of the Division of Plant Biology of the Carnegie Institution at Stanford. Clausen, working with D. D. Keck and W. M. Hiesey, initiated a series of extensive investigations into the biology of the dozen or so genera of tarweeds they recognized. These investigations continued to produce tremendously valuable and voluminous data over the next two decades. Most of this information is summarized in Clausen's *Stages in the Evolution of Plant Species* (1951).

Although little biosystematic research on the tarweeds was conducted in the 20 years following the peak of activity by Clausen, Keck, and Hiesey, another researcher, Sherwin Carlquist, began to study tarweeds from a different perspective. Carlquist's studies emphasized anatomical observations that led him to interpret the tarweeds as a rather closely knit group that includes a number of genera not previously considered to belong to the Madiinae, i.e., *Raillardella* (including *Raillardiopsis*) from western North America and *Argyroxiphium*, *Dubautia*, and *Wilkesia* from Hawaii (Carlquist, 1959). Carlquist's position on the last-mentioned three genera is of special significance because Keck (1936a, b) had specifically denied any close relationship between the Hawaiian genera and the Pacific coast tarweeds. Carlquist further stimulated interest in the Hawaiian genera in his *Hawaii, A Natural History* (1970).

Beginning about 20 years ago, biosystematic interest in the Madiinae was again on the rise. Research during this period produced a considerable amount of new biosystematic information, particularly in the Hawaiian genera and in the mainland genera *Calycadenia*, *Hemizonia*, *Holocarpha*, *Lagophylla*, and *Layia* (e.g., Carr, 1975a, b, 1977, 1985a; Carr & Carr, 1983; Carr & Kyhos, 1981, 1986; Gottlieb & Ford, 1987; Palmer, 1982; Tanowitz, 1977, 1978, 1982, 1985; Tanowitz & Adams, 1987; Thompson, 1983). The purpose of this paper is to survey briefly the diversity of the Madiinae, to summarize and integrate existing biosystematic information (some from unpublished dissertations), and to provide a preview of the results of ongoing biosystematic efforts within

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TABLE 1. Characteristics of the genera of Madiinae.

Genera	Numbers of species	Haploid chromosome numbers[1]	Descriptions[2]
PERENNIAL			
Adenothamnus	1	14	Small evergreen subshrubs, SI
Argyroxiphium	5	14	Polycarpic and monocarpic rosette shrubs, SI, SC
Dubautia	21	13(9), 14(12)	Subherbaceous mats, cushions, shrubs, trees, lianas, SI, SC?
Holozonia	1	14	Mesophytic herbs with fleshy rhizomes, SI
Raillardella	3	17(1), 17, 18?(1), 34(1)	Mat-forming or spreading scapose rhizomatous herbs of high elevations, SI
Raillardiopsis	2	7(1), 8(1)	Tufted to mat-forming rhizomatous herbs of high elevations, SI, SC?
Wilkesia	2	14	Polycarpic and monocarpic rosette shrubs, SI
TRANSITIONAL[3]			
Hemizonia	6P, 27A	9(4), 10(2), 11(4), 12(11), 13(3), 14(7)	Mostly late-flowering xerophytic herbs, the perennials subshrubby or rhizomatous, SI
Madia	2P, 18A	6(1), 7(1), 8(6), 9(3), 14(1), 16(5), 16, 24(1), 24(1)	Mesophytic to xerophytic herbs, the perennials with woody rhizomes, SC, SI
ANNUAL			
Achyrachaena	1	8	Small vernal mesophytic herbs, SC
Blepharipappus	1	8	Small xerophytic herbs, SI
Blepharizonia	1	14	Stout, xerophytic, late-flowering herbs, SI?
Calycadenia	11	4(1), 5, 6(1), 6(4), 7(5)	Mostly late-flowering xerophytic herbs, SI, SC
Holocarpha	4	4(1), 4, 5?(1), 4?, 6(1), 6(1)	Mostly late-flowering xerophytic herbs, SI
Lagophylla	4	7	Mesophytic to xerophytic herbs, SI, SC
Layia	16	7(6), 8(8), 16(1)	Vernal herbs, SI, SC
Osmadenia	1	9	Highly branched herbs, SI

[1] The information on chromosome numbers is a compilation of those given by Carlquist, 1959; Carr, 1975a, b, 1977, 1978, 1985; Clausen, 1951; Clausen et al., 1932, 1933, 1934, 1935, 1936, 1937, 1940, 1941, 1945; Johansen, 1933; Keck, 1949, 1958, 1959; Kyhos (in Carlquist, 1959); Strother (in Ferlatte, 1978), 1983; Tanowitz, 1982; Venkatesh, 1958; and previously unreported counts of $n = 12$ for *Hemizonia frutescens* A. Gray based on root tip squashes of living material collected from Guadalupe Island, Mexico by Bruce Baldwin (*Baldwin & Beauchamp 688* in DAV), and $n = 9$ for *Madia doris-nilesiae* T. W. Nelson & J. P. Nelson from bud material collected from Trinity County, California, by Barbara Williams (*Williams 518*). In genera where there is variation in chromosome numbers, the number of species with a particular chromosome constitution is given in parentheses.

[2] SC = self-compatible; SC? = self-compatible or partially so; SI = self-incompatible; SI? = self-incompatible or partially so.

[3] The two genera in this category contain perennial (P) and annual (A) species as indicated in the second column.

this fascinating group of plants. Details of other current research on the tarweeds are summarized elsewhere (e.g., flavonoid chemistry—Crins & Bohm, this volume; enzyme electrophoresis—Witter, this volume; physiological ecology—Robichaux et al., this volume; chloroplast DNA evolution—Baldwin et al., this volume).

TARWEED CHARACTERISTICS

The name tarweed refers to the often copious sticky glandular secretions produced on the surfaces of these plants, especially in the regions of the capitulescences. As viewed herein, the tarweed group (Madiinae) comprise 127 species in 17 genera, six of which are monotypic (Table 1). Seven genera are wholly perennial, eight are wholly annual, and two include annual and perennial species. While all of the 28 Hawaiian species are perennial, only 15 perennials are found among the 99 species from the Pacific coast of the Americas.

The annual species of mainland tarweeds range from about 2 cm in *Madia minima* (A. Gray) Keck to 2.5 m tall in *M. elegans* D. Don ex Lindley subsp. *densifolia* (E. Greene) Keck (Keck, 1959). The perennial mainland taxa comprise small evergreen or deciduous subshrubs and herbaceous rhizomatous taxa, some of which form extensive mats (e.g., *Raillardella* species). In contrast, the

Hawaiian taxa are exceedingly diverse and include a mat-forming subshrub, *Dubautia scabra* (DC.) Keck; a cushion plant, *D. waialealae* Rock; monocarpic and polycarpic rosette shrubs, e.g., *Argyroxiphium sandwicense* DC. subsp. *macrocephalum* (A. Gray) Meyrat and *Wilkesia hobdyi* H. St. John; woody shrubs, e.g., *D. plantaginea* Gaudich.; trees, e.g., *D. reticulata* (Sherff) Keck; and a liana, *D. latifolia* (A. Gray) Keck (Carr, 1985a).

Although there are some exceptions, the leaves of mainland tarweeds are typically narrow and somewhat linear, often grasslike in general appearance. The Hawaiian assemblage includes this type but in many species the leaves are much broader (Carr et al., 1989). The leaf veins frequently exhibit a somewhat parallel orientation that becomes extreme and exceedingly grasslike in *Wilkesia* species. However, the leaves of *Dubautia latifolia* exhibit a highly isodiametrically reticulate venation that contrasts sharply with the situation in *Wilkesia* (Carr, 1985a). In general, the leaves of vernally flowering mainland taxa such as *Layia* or plants of comparatively wet habitats in Hawaii are larger and more mesomorphic compared to those of late-flowering mainland taxa such as *Holocarpha* or Hawaiian taxa occurring in dry habitats (Carr et al., 1989). In surface area the leaves range from about 0.1 to 75 cm^2.

The flowering heads of tarweeds range from small and inconspicuous (4 mm high and less than 2 mm broad) in *Calycadenia hooveri* G. Carr and *Dubautia pauciflorula* H. St. John & G. Carr, with two or three florets per capitulum, to large and showy (35 mm tall and 60 mm broad) in *Adenothamnus validus* (Brandegee) Keck and *Argyroxiphium sandwicense* subsp. *macrocephalum*, the latter with up to 650 florets per capitulum. Almost all of the mainland taxa have radiate flowering heads, whereas in Hawaii, rays are found in the heads of only five of the 28 species. Flower colors are white, red, orange, yellow, or combinations thereof.

The mainland tarweeds occur almost exclusively in the western U.S., with their distributional center in the central valley of California. A few species extend into Mexico, and a few others are restricted to the Mexican mainland or offshore islands. Two highly disjunct species are found in South America (Chile and Argentina). The mainland perennial species are mostly quite rare and restricted in distribution, suggesting that they may be relicts of an ancestral plexus.

A second center of diversity of tarweeds is the Hawaiian archipelago, where representatives of the group occur on all of the major islands including Hawaii, Maui, Lanai, Molokai, Oahu, and Kauai. All of the tarweed species in the Hawaiian Islands are included in the Hawaiian endemic genera *Argyroxiphium*, *Dubautia*, and *Wilkesia*.

The mainland tarweeds are at home in lowland, sometimes quite xeric habitats; however, some species are found above timberline (e.g., *Raillardella argentea*); and *Madia bolanderi* (A. Gray) A. Gray typically occurs in very wet mid-elevation habitats. The Hawaiian representatives occur in tremendously diverse habitats, including recent lava flows, cinder cones, dry scrub, dry forests, mesic forests, rainforests, and bogs. Annual precipitation in these habitats ranges from about 35 cm to over 12 m. Hawaiian tarweed sites are found from near sea level to about 3,750 m elevation.

The annual mainland species generally germinate during the period of winter rains, persisting as rosettes until bolting and flowering occurs. In many species this takes place in late summer or fall, and it is not uncommon to find tarweeds flowering during October and November, or even December, before the winter rains of the following season. At the other extreme, *Achyrachaena mollis* Schauer and most species of *Layia*, among others, are vernal in their growth and flowering responses. The perennials are less predictable, although even in Hawaii they are mostly seasonal in their flowering, with summer flowering most common. A few species, such as *Dubautia knudsenii* Hillebrand, flower more or less continuously throughout the year.

As a result of the long period of intensive biosystematic research on tarweeds, the chromosome numbers are known for 122 (over 96%) of the 127 species. The only species for which no chromosome information is available are *Argyroxiphium virescens* Hillebrand (presumed extinct), *Hemizonia martirensis* Keck, *H. streetsii* A. Gray, *Layia ziegleri* Munz, and *Madia stebbinsii* T. W. Nelson & J. P. Nelson. *Calycadenia*, *Madia*, and *Hemizonia* are the most diverse in chromosome number, and together with *Raillardella*, include all of the different numbers found in the entire subtribe (Table 1). Eight of the genera have only a single confirmed chromosome number. Among the perennials, chromosome numbers are $n = 6$, 7, 8, 12, 13, 14, 17, and 34, whereas the annuals are somewhat more diverse in chromosome numbers with $n = 4$, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, and 24 (Tables 1, 2). Some species have more than one chromosome number, such as *Calycadenia pauciflora* A. Gray ($n = 5$, 6; Carr, 1975b) and *Madia gracilis* (Smith) Keck ($n = 16$, 24; Clausen et al., 1945). Mixed chromosome

TABLE 2. Distribution of Madiinae taxa in relation to gametic chromosome numbers.[1]

$n = 4$	5	6	7	8	9	10	11	12	13	14	15	16	17	24	34
			P	P										ALL SPECIES	
			P	A											
			A	A											
			A	A											
			A	A											
			A	A						18PH					
			A	A				**P**		P					
			A	A				**P**		P					
			A	A				**P**		A					
			A	A	A			**P**		A					
		P	A	A	A			**P**		**A**					
		A	A	A	A			**A**		**A**		A			
		A	A	A	A			**A**		**A**		A			
		A	A	A	A		**A**	**A**	9ph	**A**		A			
A		A	A	A	**A**		**A**	**A**	**P**	**A**		A			
A		A	A	A	**A**	**A**	**A**	**A**	**A**	**A**		A	P	A	
A	A	A	A	A	**A**	**A**	**A**	**A**	**A**	**A**		A	P	A	P
										3PH			ALL GENERA[2]		
			P	P						P					
			AP	AP						P					
		AP	A	A	AP					AP					
A		A	A	A	**AP**				ph	**AP**		A			
A	A	A	A	A	A	**AP**	**AP**	**AP**	**AP**	A		AP	P	A	P
													PERENNIAL GENERA[3]		
		AP	AP						ph	3PH					
		AP	P	P				**AP**	**AP**	P			P		P
$n = 4$	5	6	7	8	9	10	11	12	13	14	15	16	17	24	34

[1] A = annual, P = perennial, AP = both annual and perennial, PH = perennial Hawaiian taxon, ph = derived perennial Hawaiian taxon; **boldfaced** entries represent *Hemizonia*.

[2] Several genera are represented in more than one category.

[3] Includes perennial component of genera with both annual and perennial species. Some genera are represented in more than one category.

numbers showing apparent polyploid relationships within genera have turned up in *Layia*, *Madia*, and *Raillardella*.

One report of $n = 18$ for *Raillardella argentea* A. Gray from San Gorgonio Pass in southern California (Kyhos, in Carlquist, 1959) differs from those determined for this species from other locations in the Sierra Nevada ($n = 17$; Strother, 1983; $n = 17$; Kyhos, unpublished) and represents a number not otherwise known in this genus. The erroneous report of $n = 16$ by Powell & Powell (1978) for *Raillardiopsis muirii* (A. Gray) Rydb. (as *Raillardella muirii*) was apparently based on a miscommunication of the much earlier determination of $2n = 16$ by Kyhos (in Carlquist, 1959). Similarly, the report of $n = 18$ for *Raillardella argentea* by the same authors was apparently based on the earlier determination for this taxon by Kyhos (in Carlquist, 1959). Powell & Powell (1978) provided the locality and voucher information for the material on which Kyhos's determinations were made. Idiograms depicting $n = 5$ in *Holocarpha virgata* (A. Gray) Keck and $n = 4$ in *H. obconica* (Clausen & Keck) Keck by Clausen (1951) represent numbers not otherwise known for these species and need further documentation.

Very few plant groups of comparable size are better known cytologically. An examination of the pattern of distribution of the 122 species in Madiinae with known chromosome numbers reveals very prominent modes at $n = 7$ and $n = 8$, lesser modes at $n = 12$ and $n = 14$ (if one deemphasizes the monophyletic Hawaiian taxa), and minor peaks at $n = 6$, 9, and 16 (Table 2, top). This extensive and somewhat complex distribution pattern is open to various interpretations.

The pattern is simpler and less ambiguous if the chromosome number variation is considered at the generic level, where the several modes observed at the species level condense to a relatively uncomplicated pattern (Table 2, middle). This simplification is due in large measure to elimination of the influence of single-chromosome-number clusters of closely related species. This perspective at the generic level reveals more clearly how chromosome numbers correlate with major units of morphological diversity and therefore probably provides a more accurate evolutionary and systematic understanding of the Madiinae.

At the generic level the prominent modes at $n = 7$ and $n = 8$ are still present, and the only other well-developed mode is at $n = 14$ (Table 2, middle). This $n = 14$ mode consists of five quite distinct mainland genera in addition to three mutually closely related Hawaiian genera. In contrast, the $n = 16$ mode, consisting of a small cluster of closely related annual autogamous species of *Madia* and *Layia*, represents much less diversity. Of the two genera at $n = 13$, one is Hawaiian (*Dubautia*) and consists of species known to be derived from members of Hawaiian Madiinae with $n = 14$ (Carr & Kyhos, 1981, 1986) and the other is *Hemizonia*, represented by three fairly closely related species. With these three exceptions, each gametic chromosome number from $n = 10$ upward is represented by only a single genus.

Thus, the relatively simple picture that emerges at the generic level supports the view that the majority of the polyploid taxa within Madiinae are based on $n = 7$ and that although $n = 8$ is well represented at the diploid level, its polyploid derivatives are few. This suggests that $n = 7$ is of greater antiquity in the subtribe and perhaps depicts the ancestral chromosome number for Madiinae.

When *Hemizonia* is omitted from the total array of chromosome numbers (Table 2) a very large gap appears in the overall distribution of chromosome numbers, such that no taxa are represented at $n = 10$, 11, 12, and 13 (except the Hawaiian derivatives). All of the remaining species or genera fall into two quite discrete groups, one consisting of apparent diploids with gametic chromosome numbers ranging continuously from $n = 4$ to $n = 9$ and a second group composed of what appear to be polyploid taxa with gametic chromosome numbers of $n = (13)$, 14, 16, 17, 24, and 34 (Table 2). With its 33 species, *Hemizonia* is the largest genus in Madiinae, making up almost 26% of the subtribe. On this basis alone, one might predict that its removal is likely to have a pronounced effect on the overall pattern of chromosome number distribution in Madiinae. Nevertheless, it seems quite significant that the removal of no other single genus or even any combination of genera cleaves the rest of the tribe into separate diploid and polyploid groups. *Hemizonia* includes a continuous series of gametic chromosome numbers ranging from $n = 9$ to $n = 14$, and it modally centers at $n = 12$. This may indicate that the genus is primitively polyploid and that gametic chromosome numbers above and below $n = 12$ represent aneuploid derivatives from this polyploid mode.

The distribution pattern of gametic chromosome numbers of the perennial genera within Madiinae is quite similar to that of the entire subtribe (Table 2, bottom). When the perennial taxa are examined at either the specific or generic level, a small mode appears at $n = 7$ and a more prominent mode is present at $n = 14$. If one accepts the reasonable assumption that the ancestral taxa to the tribe are more likely to have been perennials, it seems particularly significant that the chromosome number distribution of the extant perennials conforms to the previous pattern observed for the entire subtribe in that the polyploids are concentrated at $n = 14$ and thus appear to be based principally on $n = 7$, not on $n = 8$. This interpretation is supported further by the total absence of perennial taxa with $n = 16$. On the other hand, the possibility cannot be dismissed that the prominence of $n = 14$ taxa within the subtribe may at least in some cases be the result of the combination of diploid species with $n = 6$ and $n = 8$ to produce polyploids at $n = 14$. This possibility is strengthened by preliminary evidence obtained from hybridization experiments involving the Hawaiian and mainland Madiinae (Baldwin, 1989; Baldwin et al., unpublished).

Infrageneric Cytogenetic Relationships

With the exceptions of *Wilkesia* and monospecific genera, one or more interspecific hybrids have been produced in all of the tarweed genera. The cytogenetic information on these hybrids is summarized below according to the sequence of genera in Table 1.

Genera with perennial species only

Argyroxiphium. *Argyroxiphium* comprises five perennial species, all with $n = 14$ (Table 1). Only the interspecific combination *A. grayanum* (Hillebrand) Degener × *A. sandwicense* subsp. *sandwicense* has been produced (Carr & Kyhos, 1986). The two F_1 individuals available for analysis

averaged 63% pollen stainability and consistently produced 12 pairs and one chain or ring of four chromosomes at meiosis, indicating heterozygosity for a single reciprocal chromosome translocation. In spite of its heterozygosity, this hybrid functioned well as a male and as a female parent in the production of an intergeneric recombinant involving *Dubautia linearis* (Gaudich.) Keck. Self-incompatibility has been demonstrated in *A. sandwicense* (Carr et al., 1986).

Dubautia. The wholly perennial genus *Dubautia* includes nine species with $n = 13$ and 12 species with $n = 14$ (Table 1). A total of 41 different interspecific hybrid combinations, 11 of them occurring in nature, have been available for study (cf. Carr & Kyhos, 1986). Chromosome structural stability among the 13-paired species of the genus is indicated by the consistent meiotic display of 13 pairs of chromosomes and high pollen stainability (96% or greater) of all interspecific hybrid combinations involving these species. The close relationship between the genome of *D. scabra* ($n = 14$) and the 13-paired genome is demonstrated by consistent production of 12 pairs and one chain of three chromosomes during meiosis and the high pollen stainability averaging 81% in 29 individuals of seven different interspecific combinations involving *D. scabra* and 13-paired species. Cytogenetic, biogeographic, and morphological evidence, as well as information from isozyme studies (Witter, this volume; Witter & Carr, 1988) support the conclusion that the 13-paired species represent a monophyletic group comparatively recently derived via aneuploid reduction of chromosomes from the $n = 14$ genome possessed by *Dubautia scabra*.

Unlike the 13-paired genome, the 14-paired genome is not structurally uniform. Biosystematic studies have so far revealed four $n = 14$ chromosome structural cytotypes comprising one or more highly morphologically differentiated species that differ from one another by a minimum of one or two reciprocal translocations, as indicated by the meiotic configurations in different interspecific hybrid combinations. Pollen stainability in these hybrids ranges from 27% to 42% and appears to be determined largely by the complexity and behavior of the multiple chromosome associations. A single univalent chromosome resulting from chiasma failure in one of the chromosome multiples may be seen in a low frequency of meiocytes in some of these hybrids. The cytogenetic evidence indicates that a limited number of chromosomes have been repeatedly involved in separate translocation events to produce the observed spectrum of cytotypes.

It has been possible to create a number of hybrid products beyond the F_1 generation. In one instance, two interspecific hybrids involving species with the same chromosome structural arrangement were crossed to produce a hybrid product combining the four species *Dubautia knudsenii*, *D. laxa* Hook. & Arn., *D. microcephala* Skottsb., and *D. plantaginea*. In another example, three chromosomally differentiated species, *D. knudsenii* ($n = 14$), *D. latifolia* ($n = 14$), and *D. sherffiana* Fosb. ($n = 13$) were combined in two successive hybridizations. Clearly, results to date suggest that it is possible to hybridize and potentially to recombine virtually any combination of species in the genus regardless of their exceedingly diverse morphological and chromosomal attributes. Self-incompatibility and self-compatibility occur in the genus (Carr et al., 1986).

Raillardella. Three perennial species comprise the genus *Raillardella* (Table 1). Two interspecific hybrid combinations, *R. pringlei* E. Greene ($n = 17$) × *R. scaposa* A. Gray ($n = 34$) and *R. pringlei* × *R. argentea* (A. Gray) A. Gray ($n = 17$), have been produced (Baldwin, 1989). At meiosis the first hybrid exhibited a mixture of univalents, bivalents, trivalents, and possibly larger chromosome multiples, whereas the second hybrid exhibited only normal meiotic bivalents. Experience with cultivated plants suggests that all three species in the genus are self-incompatible.

Raillardiopsis. *Raillardiopsis* consists of two perennial species. One hybrid between *R. muirii* ($n = 8$) and *R. scabrida* (Eastw.) Rydb. ($n = 7$) exhibited mostly univalents and chains of chromosomes at meiosis. The spectrum of multiple associations observed in the hybrid indicates that the parental genomes are differentiated by at least three chromosome translocations (Baldwin, 1989). Stainable pollen grains in this hybrid (9%) were mostly four-colporate, suggesting a derivation from unreduced meiocytes. Experimental manipulations indicate that *R. muirii* is self-incompatible (Baldwin & Kyhos, in press) and suggest that *R. scabrida* may have limited self-compatibility.

GENERA WITH PERENNIAL AND ANNUAL SPECIES

Hemizonia. The largest genus of Madiinae is *Hemizonia* with 27 annual and six perennial species (Table 1). The perennial species are all highly restricted in distribution and most are quite rare. They occur principally on the offshore islands of

southern California and Baja California Norte, although *H. minthornii* Jepson and *H. perennis* (E. Greene) Keck are confined to the mainland in coastal and near-coastal habitats. The otherwise insular *H. greeneana* Rose has a narrowly restricted extension on the mainland of Baja California at Punta Banda. Nearly all of the annual species of *Hemizonia* are confined to the mainland of California, with a few extending into the adjacent western states and Mexico. In contrast to the characteristically rare and restricted perennial species, which appear to be relictual, many of the annual species of *Hemizonia* are quite common, relatively widespread, and thus apparently vigorous, recently evolved entities.

Most of what is known biosystematically about *Hemizonia* has been derived from the extensive research conducted by Clausen, Keck, and Hiesey in the first half of this century (Clausen, 1951). Subsequently, Tanowitz (1977, 1978, 1982, 1985) generated additional biosystematic information for the genus. The species of *Hemizonia* appear to form four rather natural species groups or sections, which have been given various names by different taxonomists. Section *Hemizonia* (formerly sect. *Euhemizonia*) consists of seven species, each with 14 pairs of chromosomes, which sets them apart from all other species in the genus. The Carnegie research team found that these seven species could all be intercrossed easily and that their hybrids represent the most fertile interspecific combinations in *Hemizonia*. Section *Centromadia*, commonly known as the spikeweeds, is an obviously natural group of four or so species that can all be intercrossed readily to produce hybrids of moderate fertility in most cases. The Carnegie research team studied four annual species of this section. These few species were found to possess a surprisingly extensive series of chromosome numbers (n = 9, 11, 12, and 13). One extremely rare spikeweed, *H. perennis*, which apparently was unknown to Clausen's research group, is a rhizomatous perennial and has subsequently been investigated experimentally. It has 13 pairs of chromosomes and the ability to cross with the annual spikeweeds to produce vigorous hybrids generally with rather low fertility (Kyhos, unpublished). The third species group within *Hemizonia* consists of all the remaining annual species. These have gametic chromosome numbers that range continuously from n = 9 to n = 13. The fourth species group consists of five of the six perennial species (excluding *H. perennis*) discussed above. This group is characterized by the chromosome number n = 12.

The view that emerges from these experimental studies is that most interspecific crosses within this genus produce hybrids with low to extremely low fertility (see fig. 62, Clausen, 1951). Interspecific hybrids with normal to near normal fertility are exceptional. Often the reduced fertility appears to result from chromosome differences between the species, but in some instances genetic factors are likely to be responsible. Almost half of the more than 55 interspecific combinations produced by the Carnegie research effort were highly sterile hybrids. Most of the remaining hybrid combinations had substantially depressed fertility. Intersectional hybrids typically were extremely sterile, with but a single exception involving *H. pungens* (Hook. & Arn.) Torrey & A. Gray and *H. ramosissima* Benth. (*H. fasciculata*). Some 20 interspecific hybrid combinations attempted by the Carnegie research team failed. Thus experimental evidence reveals strong reproductive barriers between most *Hemizonia* species.

A high degree of chromosome repatterning within *Hemizonia* is clearly indicated by an extensive series of chromosome numbers, which range continuously from n = 9 to n = 14. The annual species show the greatest diversity with their members spanning this entire series. The perennials are much more limited, with five of their six species having n = 12, and the remaining species, *H. perennis*, with n = 13. Unquestionably, chromosome evolution has played a major role in the evolution of the genus.

Madia. *Madia* includes some 20 species (18 annuals). The modal chromosome number is n = 8, but numbers of n = 9, 14, 16, and 24 are also found among the annual species (Table 1). The two rhizomatous perennial species, *M. madioides* (Nutt.) E. Greene (n = 7) and *M. bolanderi* (n = 6), are chromosomally unique within the genus. As with *Layia*, nearly all in-depth biosystematic knowledge of *Madia* stems from Clausen, Keck, and Hiesey (Clausen, 1951). They produced 22 interspecific hybrid combinations among the 14 species in their crossing program. Their research revealed that the diploid species generally are strongly isolated from one another reproductively; this isolation often seems to be associated with chromosome repatterning, as is evident from the diversity of chromosome numbers in *Madia*. Some polyploid species retain substantial ability to exchange genes.

GENERA WITH ANNUAL SPECIES ONLY

Calycadenia. This genus comprises 11 annual species with chromosome numbers ranging from n

= 4 to $n = 7$ (Table 1). Seventeen interspecific hybrid combinations have been examined (Carr, 1975a, 1977). Hybrids among the seven-paired species *C. mollis* A. Gray, *C. truncata* DC., and *C. villosa* DC. are very sterile, exhibiting less than 1% stainable pollen grains, and are characterized by very low meiotic pairing of chromosomes. The hybrid between the two seven-paired species *C. villosa* and *C. hooveri* also has less than 1% stainable pollen but often produces five pairs and one ring or chain of four chromosomes, indicating heterozygosity for a reciprocal chromosome translocation. This hybrid was also heterozygous for at least one paracentric inversion, as indicated by bridge and fragment configurations in 26% of the meiocytes. Hybrids among *C. ciliosa* E. Greene ($n = 6$), *C. hispida* (E. Greene) E. Greene ($n = 6$), *C. multiglandulosa* DC. ($n = 6$), *C. pauciflora* ($n = 5, 6$), *C. oppositifolia* (E. Greene) E. Greene ($n = 7$), and *C. spicata* (E. Greene) E. Greene ($n = 4$) are characterized by strict meiotic bivalent formation or, more frequently, large multiple associations of chromosomes, indicating structural heterozygosity for three or more reciprocal chromosome translocations in some cases. Pollen stainability in these hybrids ranged from less than 1% to 69%. A single hybrid between the seven-paired *C. villosa* and a six-paired representative of *C. pauciflora* had a pollen stainability of less than 1%. Based on a maximum meiotic association of nine chromosomes and the appearance of bridge and fragment configurations in 66% of the meiocytes of this hybrid, it was heterozygous for at least three reciprocal chromosome translocations and probably multiple paracentric inversions.

Two closely related species complexes, *Calycadenia hispida–C. multiglandulosa* and *C. ciliosa–C. pauciflora*, exhibit very different modes of evolution. The former complex is made up of five morphologically differentiated but chromosomally stable and highly interfertile taxa, while the latter complex comprises at least eleven mostly somewhat morphologically cryptic chromosome races differentiated from one another by reciprocal chromosome translocations and in some cases at least one pericentric inversion (Carr, 1975b, 1977; Carr & Carr, 1983). There appear to be no significant differences in reproductive biology, numbers of chromosome mutations detected in field populations, habitats, flowering times, or chiasma frequencies that might provide a basis for the very different modes of evolution observed in these two species complexes. These differences may be attributable to the importance of gene position (pattern) effects and/or gene linkage effects in producing optimum genomic arrangements in these plants (Kyhos & Carr, unpublished).

Over 500 interpopulational hybrids in more than 300 progenies have led to the recognition of four homoploid races ($n = 6$) and one heteroploid race ($n = 5$) in *Calycadenia pauciflora* and five homoploid races in *C. ciliosa* ($n = 6$) (Carr, 1975b; Carr & Carr, 1983). Ongoing research with additional hybrids indicates further unresolved complexity in *C. ciliosa* and one additional race ($n = 6$) of *C. pauciflora* (Carr & Carr, unpublished). The evidence suggests that a six-paired race of *C. pauciflora* arose from *C. ciliosa*, underwent additional chromosome repatterning, and ultimately produced the five-paired race by aneuploid reduction.

The research with *Calycadenia ciliosa* has revealed extremely high levels of chromosome structural heterozygosity among individuals of three populations. In one population, 30% of the plants sampled were heterozygous for one or two translocations or a pericentric inversion. In another population, morphologically indistinguishable plants within 100 m of one another were differentiated by a minimum of four reciprocal chromosome translocations (Carr & Carr, 1983).

Other current research reveals the presence of at least three structurally differentiated genomes in *C. truncata*. Extensive biosystematic manipulations with all species of the genus have demonstrated strict self-incompatibility in all but *C. hooveri* and one population of *C. truncata*.

Holocarpha. Despite being a small genus of four annual species, the taxa of *Holocarpha* present a very complex situation in terms of chromosome repatterning and reproductive isolation. This extreme complexity was first revealed by Clausen, Keck, and Hiesey in the 1930s and 1940s (Clausen, 1951). The initial indication of the complexities within this genus was the discovery that *H. macradenia* (DC.) E. Greene and *H. virgata* have a chromosome number of $n = 4$, whereas *H. obconica* and *H. heermannii* (E. Greene) Keck have $n = 6$. It was further recognized that three of these species, exempting *H. macradenia*, displayed considerable intraspecific karyotypic variation, indicative of substantial chromosome evolution among and within the species. Clausen (1951) expressed the opinion that the rare *H. macradenia* had probably already become extinct, which may be the reason it was not studied more thoroughly.

However, subsequent research by Palmer (1982) revealed that *H. macradenia*, although near extinction, survived in seven small, widely scattered

populations in the San Francisco Bay and Monterey Bay regions. Five of these relict populations remain today. Palmer showed that the then-extant seven relict populations were cross-compatible, interfertile, and in possession of the same chromosome arrangement, with the exception of a single population near Santa Cruz. This exceptional population differs from the others primarily by a chromosome translocation, with a second translocation also possibly present in some members of the population. All tested individuals of *H. macradenia* are self-incompatible, as are the other three species of *Holocarpha*. Some populations of the chromosomally diverse *H. virgata* differ from the modal chromosome arrangement of *H. macradenia* by only a single translocation and thus produce interspecific hybrids with *H. macradenia* that are upward of 80% fertile.

Palmer's (1982) research also revealed a fairly close relationship between *H. macradenia* ($n = 4$) and *H. heermannii* ($n = 6$) in that their interspecific hybrid at meiosis forms a chromosome pairing configuration of a multiple of six and multiple of four. Similarly, Palmer turned up a close relationship between *H. macradenia* and *H. obconica* ($n = 6$), their interspecific hybrid producing a configuration of three pairs and a multiple of four chromosomes at meiosis.

Lagophylla. This is a small genus of four annual species, all with a chromosome number of $n = 7$. Biosystematic investigations (Thompson, 1983) showed these species to be differentiated from one another by one or two reciprocal chromosome translocations and in some instances by inversions. This relatively modest amount of chromosome repatterning seems to be responsible for the reduced fertility observed in all interspecific hybrids. Fertility in these hybrids modally ranges from values as low as 15% to 25% in some interspecific combinations to as high as 40% to 60% in others. *Lagophylla dichotoma* Benth., *L. glandulosa* A. Gray, and *L. minor* (Keck) Keck are self-incompatible, whereas *L. ramosissima* Nutt. readily selfs in cultivation and presumably in nature. Correlated with these breeding system differences, *L. ramosissima* failed to serve as a successful pollen parent in experimental hybridizations but did function quite well as a pistillate parent when care was taken to prevent selfing. This sort of unilateral interspecific incompatibility has been repeatedly observed between self-incompatible and selfing taxa among members of Compositae.

Species of *Lagophylla* appear to have the most specialized floral features of the entire subtribe. All populations of *Lagophylla* always possess 11 florets per capitulum, five of which are ray florets, and the remaining six are disk florets arranged as a concentric ring of five florets encircling a single central disk floret. The ray florets are strictly pistillate, whereas the disk florets are only pollen fertile, never producing viable fruits. The flowers of *Lagophylla* species open in the morning and are typically closed by midday. Within the entire Madiinae this constellation of floral features occurs only in *Lagophylla*.

Layia. This entirely annual genus contains some 16 species with chromosome numbers of $n = 7$, 8, and 16 (Table 1). Most of the existing biosystematic knowledge of this genus was accumulated by Clausen, Keck, and Hiesey (Clausen, 1951). They produced 24 different interspecific hybrid combinations among 13 of the 14 species in their crossing program. Although very little detailed information was presented, they attributed the broad spectrum of reduced fertilities of the hybrids to the presence of variable numbers of unpaired chromosomes.

Tanowitz & Adams (1986) studied naturally occurring hybrids between the polytypic, obligately outcrossing *Layia glandulosa* (Hook.) Hook. & Arn. ($n = 8$) and the relatively uniform, self-compatible *L. paniculata* Keck ($n = 16$). As expected, this triploid hybrid has a low fertility of less than 6% and appears incapable of exchanging genes with its two parental species. The modal meiotic chromosome configuration of the triploid hybrid is eight bivalents plus eight univalents, which was interpreted as evidence that the two parental species share a common genome. An alternative interpretation based on the possibility of autosyndetic pairing among the chromosomes of *L. paniculata* is also tenable.

In-depth comparative investigations by Ford and Gottlieb involving research into the genetics and associated developmental processes of the rare serpentine endemic *L. discoidea* Keck and its probable ancestor *L. glandulosa* greatly extend the original research of Clausen, Keck, and Hiesey (Gottlieb & Ford, 1987; Ford & Gottlieb, 1989).

Intergeneric Cytogenetic Relationships

Argyroxiphium × *Dubautia.* Four different intergeneric F_1 hybrid combinations involving genomes 1 and 2 of *Argyroxiphium* ($n = 14$) and genomes 1, 2 (both $n = 14$), and 5 ($n = 13$) of *Dubautia* have been analyzed (Carr & Kyhos, 1986). Meiosis in each of these hybrids is characterized by a very high frequency of normal chromosome pairing and one or more multiple chro-

mosome associations. The results indicate that the parental genomes are differentiated by two or three translocations, and by aneuploidy in the hybrids involving *Dubautia* genome 5. The mean pollen stainabilities of these hybrids range from 11% to 29%. The least fertile of these, *A. sandwicense* subsp. *macrocephalum* ($n = 14$) × *D. menziesii* (A. Gray) Keck ($n = 13$), occurs in nature and produces backcrosses under field conditions. A synthetic intergeneric hybrid combining the genomes of *D. knudsenii*, *D. laxa*, and *A. sandwicense* subsp. *macrocephalum* was produced and subsequently crossed with *D. scabra* to yield a hybrid product combining the genomes of four species (Carr & Kyhos, unpublished). In another instance, a hybrid between genomes 1 and 2 of *Argyroxiphium* ($n = 14$) was successfully crossed with genome 5 ($n = 13$) of *Dubautia* (Carr & Kyhos, 1986).

Argyroxiphium × *Wilkesia.* Two hybrid combinations have been produced (*A. sandwicense* subsp. *macrocephalum* × *W. gymnoxiphium* A. Gray and *A. grayanum* × *W. hobdyi*), but neither has yet furnished material for meiotic analysis.

Calycadenia × *Osmadenia.* *Osmadenia tenella* Nutt. has been successfully crossed with *Calycadenia truncata*, *C. mollis*, and *C. villosa* (Carr, 1977). Observations of meiosis in the last-mentioned two combinations demonstrate essentially complete lack of pairing of the parental genomes. The chromosomes of *Osmadenia* ($n = 9$) are much smaller than those of the seven-paired species of *Calycadenia*, and these size differences were very apparent at meiosis in the two intergeneric hybrid combinations examined. The hybrids exhibited less than 1% pollen stainability.

Dubautia × *Raillardiopsis.* Recently, *D. laevigata* A. Gray ($n = 14$) was successfully crossed with *R. muirii* ($n = 8$) (Baldwin, 1989; Baldwin et al., unpublished). This represents the first hybrid produced between Hawaiian and mainland tarweeds. The cross was easy to make and the hybrids are vigorous. Analysis of root tips of the hybrids indicates that $2n = 22$ and verifies their parentage.

Dubautia × *Wilkesia.* Hybrids between *W. gymnoxiphium* or *W. hobdyi* and *Dubautia* genomes 1 and 4 have consistently yielded a high frequency of normal pairs and either two chains of three or one chain of six chromosomes (Carr & Kyhos, 1986). The mean pollen stainability is about 29%. One or occasionally two univalents may be found in cells exhibiting incomplete synapsis of the members of the chains of three chromosomes. Univalents of a similar origin were fairly commonly observed in a small sample of meiotic material from a hybrid between *W. gymnoxiphium* and *D. herbstobatae* G. Carr ($n = 13$). Maximum chromosome associations in this hybrid indicate that at least two translocations differentiate the parents, as is the case in the previous examples. However, an additional chain of three chromosomes represents the aneuploid relationship of the parents in this instance. Pollen stainability of this hybrid was 16% (Carr & Kyhos, unpublished).

Hemizonia × *Holozonia.* The very brief report by Clausen et al. (1937) of this intergeneric combination based on *Hemizonia arida* Keck ($n = 12$) × *Holozonia filipes* (Hook. & Arn.) E. Greene ($n = 14$) appears to have been overlooked by most recent tarweed workers. Aside from noting that it is a remarkable combination involving an annual and a perennial species, Clausen et al. (1937, p. 212) did little more than characterize it as "a vigorous but sterile hybrid grown in 1937."

Layia × *Madia.* Two hybrid combinations have been made (Clausen, 1951). The first, *M. elegans* ($n = 8$) × *L. platyglossa* (Fischer & C. Meyer) A. Gray ($n = 7$), was extremely weak and apparently did not yield cytogenetic data. The second, *M. sativa* Molina ($n = 16$) × *L. platyglossa* ($n = 7$), although fairly vigorous, was highly sterile as a result of its being a triploid with 23 somatic chromosomes.

Madia × *Raillardiopsis.* Only one combination, *M. bolanderi* ($n = 6$) × *R. muirii* ($n = 8$) has been produced (Baldwin, 1989). Hybrids of this combination exhibit a mixture of chromosome pairs, multiples, and univalents during meiosis. The multiples observed indicate that the parental genomes are differentiated by at least two reciprocal chromosome translocations. Pollen stainability of two individuals averaged 7%.

Raillardella × *Raillardiopsis.* The single hybrid combination produced, *Raillardella pringlei* ($n = 17$) × *Raillardiopsis muirii* ($n = 8$), exhibited mostly univalents at meiosis. Only a low frequency of cells yielded one or two pairs of chromosomes. The chromosomes fall roughly into two size classes with about eight (presumably those of *Raillardiopsis muirii*) in the large size class. The pollen stainability of this hybrid is 1% (Baldwin, 1989).

Discussion

Infrageneric biosystematic and cytogenetic studies indicate that variation in chromosome number and/or structure occurs in all ten of the genera

with more than one species that have been investigated. It is clear that repatterning of chromosomes has been a very significant aspect of the overall differentiation of the tarweeds, but chromosomal and morphological diversification have frequently proceeded at very different rates. In some cases, as in *Calycadenia*, chromosomal differentiation has been pervasive and has accrued even among forms that are otherwise exceedingly similar, if not indistinguishable (Carr, 1977; Carr & Carr, 1983). Certain chromosomes have been repeatedly involved in translocations in *Calycadenia* (Carr, 1975b; Carr & Carr, 1983) and *Dubautia* (Carr & Kyhos, 1986). By comparison, the chromosomes of *Lagophylla* exhibit only modest infrageneric variation in structure (Thompson, 1983). Overall, the kinds of chromosome evolution that have been documented within the Madiinae include aneuploidy, polyploidy, and structural differentiation by way of reciprocal translocations and pericentric and paracentric inversions.

Nine different intergeneric hybrid combinations have been produced. Of the six that have been examined, pollen stainability ranges from less than 1% to 29%. Meiotic chromosome associations among the intergeneric hybrids range from essentially all univalents in most meiocytes of *Calycadenia* × *Osmadenia* to exclusively pairs and multiples in most meiocytes of *Argyroxiphium* × *Dubautia*. There appears to be very little potential for intergeneric gene flow, especially under field conditions, except between the Hawaiian genera *Argyroxiphium* and *Dubautia*.

The relatively high fertility among the Hawaiian taxa could be used to argue for their treatment as congeners. However, the three Hawaiian genera recognized here are easily distinguished and conform well to generic concepts used elsewhere in the Asteraceae (Carr, 1985b). Moreover, the argument used to reduce these taxa to a single genus could logically be extended to reduce them to a single species, an extension that even the most strict adherents to the biological species concept would have to question.

Two of the intergeneric hybrids briefly reported here establish a closeness of relationship not previously perceived for the genera involved. Furthermore, the degree of chromosome association and fertility in the first of these hybrids, *Madia* × *Raillardiopsis*, suggests that a taxonomic realignment may prove necessary. The second of these hybrids, *Dubautia laevigata* × *Raillardiopsis muirii*, establishes a direct genetic link between the mainland and Hawaiian tarweeds. Attempts to produce both hybrids were encouraged by results from a cpDNA study that indicated very close relationship among *Madia bolanderi*, *Raillardiopsis muirii*, and the Hawaiian taxa (Baldwin, 1989; Baldwin et al., this volume). These hybrids provide the opportunity to explore the derivation of what may very well be the ancestral genomes of the entire assemblage of Hawaiian Madiinae. This may be an exciting new chapter in the rich history of biosystematic and other experimental research on the tarweeds. As Jens Clausen used to say, "We have only just begun to scratch the surface."

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CHLOROPLAST DNA EVOLUTION AND ADAPTIVE RADIATION IN THE HAWAIIAN SILVERSWORD ALLIANCE (ASTERACEAE–MADIINAE)[1]

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Abstract

Chloroplast DNA (cpDNA) restriction site variation among 24 of 27 extant species of the Hawaiian silversword alliance (*Argyroxiphium, Dubautia, Wilkesia*) was studied to enhance understanding of phylogenetic patterns and evolutionary processes in this outstanding example of insular adaptive radiation. Analysis with 16 restriction endonucleases revealed a total of 55 restriction site differences, 36 being shared by a subset of at least two taxa. In pairwise comparisons among these taxa, cpDNA divergence ranged from 0 to 0.46% of nucleotides. Chloroplast DNA divergence within *Dubautia* exceeded that of all intergeneric comparisons. A strict consensus tree from Wagner parsimony analyses of this variation was topologically congruent with evolutionary resolutions from Dollo parsimony and the Fitch-Margoliash genetic distance algorithm. Conflict between these outcomes and results from a phenetic analysis suggest a cpDNA molecular clock is not operating among these taxa. The cpDNA consensus phylogeny indicates monophylesis of the silversword alliance, in accord with biosystematic and cytogenetic evidence. These data further suggest: (1) rapid radiation of lineages early in the history of the silversword alliance; (2) few successful interisland migrations that led to new species lineages; (3) a unidirectional, older-to-younger island pattern of migration within the $n = 13$ *Dubautia* group; (4) striking inconsistency between relative rates of morphological and cpDNA evolution among *Wilkesia* and five Kauaian *Dubautia* species; and (5) hybrid speciation or extensive introgression among certain *Argyroxiphium* and *Dubautia* taxa. These phylogenetic conclusions require testing with molecular analyses of nuclear DNA to clarify the extent to which hybridization has influenced the evolution of this reproductively and genetically cohesive group of plants.

Prominent examples of insular adaptive radiation are widely acknowledged as exceptional demonstrations of organismic evolution. Indeed, these groups of seemingly closely related species are characterized by levels of phenotypic diversity otherwise associated with higher taxa (e.g., Hawaiian Drepanidae, Galápagos Geospizinae). Evolutionary studies of such systems hold great potential to provide unique insights into mechanisms of evolution, origins of major organismic lineages, and genetic bases of conspicuous or fundamental characteristics.

Despite extensive documentation of island plant life (e.g., Carlquist, 1965, 1974), few biosystematic or "experimental" data from insular floras are available. For example, only a small fraction of the Hawaiian archipelago flora has been thus examined to any degree (Carr, 1987). This is unfortunate, given the increasingly precarious position of island ecosystems and the importance of understanding phylogeny for evolutionary interpretations.

In plants, molecular phylogenetic approaches employing DNA appear to be especially suited to the study of insular adaptive radiation. Previous investigations of continental plant groups using chloroplast DNA (cpDNA) have revealed convincing evidence of relationships obscured by morphological evolution (reviewed in Sytsma & Smith, 1988; Palmer et al., 1988). Molecular insight is needed in studies of island species given their apparent potential for rapid morphological change, parallelism, and hybridization.

The Hawaiian silversword alliance represents an

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ideal island plant assemblage for DNA systematic study. Comprising only 28 species in three distinctive genera (*Argyroxiphium*, *Dubautia*, and *Wilkesia*), this manageably small group spans an exceptional range of diversity in morphological, anatomical, and ecological characteristics (Carr, 1985). In fact, Carlquist (1974) regarded the silversword alliance as the most outstanding example of angiosperm adaptive radiation in the Hawaiian archipelago.

The extensive background of evolutionary research on these plants includes anatomical (Carlquist, 1957, 1958a, b, 1959a, b; Kim, 1987), cytogenetic (Carr & Kyhos, 1981, 1986), isozymic (Witter, 1986; Witter & Carr, 1988), ecophysiological (Robichaux, 1984, 1985; Robichaux & Canfield, 1985), chemosystematic (Crins et al., 1988), and breeding system (Carr et al., 1986) investigations. These studies clearly delimit Hawaiian Madiinae and indicate their evolutionary cohesiveness. For example, artificial and natural hybridization have linked nearly all species, the F_1 generations being of at least marginal fertility in every instance (Carr & Kyhos, 1981, 1986). Most importantly for DNA phylogenetic analysis, a closely related lineage that is ancestral to the silversword alliance has been identified by chloroplast DNA investigations and interspecific hybridization involving perennial North American Madiinae (Baldwin, 1989). These studies led to recognition of two outgroup species with close affinities to Hawaiian Madiinae: *Madia bolanderi* and *Raillardiopsis muirii*.

In this paper, we present results from a DNA systematic study of restriction site polymorphisms in the silversword alliance. Chloroplast DNA (cpDNA) was selected for analysis for three reasons: (1) evolutionary interpretation of uniparentally inherited cpDNA is essentially free from the complexities resulting from sexual processes encountered in nuclear DNA (reviewed in Birky, 1988); (2) unlike plant mitochondrial DNA, cpDNA is in most cases structurally conservative and evolves more rapidly by point mutations (Palmer, 1985), facilitating restriction site analysis; and (3) all previous genetic studies of the silversword alliance have focused on the nuclear genome or its expression. A uniparental phylogeny was desired to resolve better the role of hybridization in the evolution of these interfertile species.

Materials and Methods

Fresh leaves were field- or greenhouse-collected from representatives of one to five populations of 24 of the 27 extant silversword alliance species and from two outgroup taxa of North American Madiinae, *Madia bolanderi* and *Raillardiopsis muirii* (Table 1). Leaves were ground in liquid N_2 with mortar and pestle. Total DNA was isolated from these leaf N_2 powders and purified twice on cesium chloride gradients using a modified procedure of Palmer (1986), omitting separation of organelles. Mercaptoethanol was increased up to 1% in the extraction buffer to increase the solubility of mucilaginous carbohydrates. DNA aliquots from one or two populations of each species were digested with each of 16 restriction endonucleases recognizing four, five, or six nucleotide-pair sites (Table 3). "Six-cutter" enzymes with AT-rich recognition sites were chosen to maximize cleavage of the AT-rich cpDNA molecule. Resulting cpDNA fragments were resolved in 1.25–4% agarose gels by Southern blot hybridization with ^{32}P-labeled cpDNA sequences. Probes were prepared by extension of random primers (Amersham) annealed to gel-isolated inserts from clones of a *Sac* I *Lactuca* cpDNA library, generously provided by R. K. Jansen and J. D. Palmer, and a 9.0 kb *Pst* I *Petunia* fragment (J. D. Palmer and E. Clark), obtained through K. J. Sytsma. Together these probes represented >99% of the lettuce cpDNA molecule (Fig. 1). Partial restriction mapping of cpDNA from four Hawaiian species with three enzymes revealed no deviations in cpDNA size or structure relative to lettuce (Baldwin et al., unpublished). Restriction site changes were interpreted with reference to standard markers of triple-digested (*Bam* HI, *Eco* RI, *Hind* III) and single-digested (*Hind* III) lambda phage DNA. Length mutations were distinguished from restriction site mutations near preexisting sites by comparisons of all digests at the region in question.

Both Wagner and Dollo parsimony were employed in cladistic phylogenetic analyses of the restriction enzyme data set. Wagner parsimony treats all mutations equivalently, whereas Dollo parsimony prohibits certain evolutionary parallelisms—parallel restriction site gains and loss/gains—the least probable homoplasious changes (DeBry & Slade, 1985). A presence/absence matrix of all restriction sites shared by a subset of two or more taxa, including the outgroup species, was analyzed by Wagner parsimony using the PAUP package, version 2.4 (D. L. Swofford, Illinois Natural History Survey). The GLOBAL and MULPARS branch-swapping options and the branch-and-bound (BANDB) option of PAUP were used to search for the shortest topologies. A strict consensus tree of the maximally parsimonious reso-

TABLE 1. Collections of species analyzed for chloroplast DNA restriction site polymorphisms. DNA samples from a given location comprised one individual unless indicated by "(P)" = pooled sample of two to ten individuals from one population. Lowercase letter designations following voucher numbers indicate separate clusters of individuals within a population. Collection numbers in parentheses indicate accessions screened only for select mutations found in the main analysis (see "Materials and Methods"). Collector abbreviations are: *BGB* = *B. G. Baldwin et al.*; *GDC* = *G. D. Carr*. Vouchers are at DAV (*BGB* and *A. Medeiros* collections) or HAW (other collections) unless specifically indicated. [1] (BISH, HAW, US). [2] (PTBG). [3] (BISH, F, US). [4] (BISH, F, HAW, US). [5] (BISH).

Argyroxiphium caliginis C. Forbes—*BGB 660*, Pu'u Kukui, West Maui.

Argyroxiphium grayanum (Hillebrand) Degener *BGB 661*, Pu'u Kukui, West Maui; *A. Medeiros s.n.*, Haleakala, East Maui.

Argyroxiphium sandwicense DC. subsp. *macrocephalum* (A. Gray) Meyrat—(*GDC 1239*), Haleakala, East Maui.

Argyroxiphium sandwicense DC. subsp. *sandwicense*—*BGB 657* (P), upper Wailuku drainage, Mauna Kea, Hawaii.

Dubautia arborea (A. Gray) Keck—*BGB 527* (P), Pu'u La'au, Mauna Kea, Hawaii; (*BGB 656*), upper Wailuku drainage, Mauna Kea, Hawaii.

Dubautia ciliolata (DC.) Keck subsp. *ciliolata*—*BGB 529* (P), Crater Rim Trail, Kilauea, Hawaii.

Dubautia ciliolata (DC.) Keck subsp. *glutinosa* G. Carr—(*BGB 525*) (P), near Pu'u Huluhulu, Hawaii; (*BGB 659*), upper Wailuku drainage, Mauna Kea, Hawaii.

Dubautia herbstobatae G. Carr—*GDC 1244*, Ohikilolo Ridge, Waianae Range, Oahu.

Dubautia imbricata H. St. John & G. Carr subsp. *imbricata*—*BGB 667*, Wahiawa Mountains, Kauai.

Dubautia knudsenii Hillebrand subsp. *filiformis* G. Carr—(*GDC 1234*), Makaleha Mountain, Kauai.

Dubautia knudsenii Hillebrand subsp. *knudsenii*—*GDC 1047*, Awaawapui Trail near Kokee Road, Waimea, Kauai; (*GDC 946*[1]) (P), Kahuamaa Flat, Kokee Park, Kauai.

Dubautia knudsenii Hillebrand subsp. *nagatae* (H. St. John) G. Carr—(*GDC 1322*a, b) (P), Pihea Trail, Alakai Swamp, Kauai.

Dubautia laevigata A. Gray—*BGB 671*, Kaluapuhi Trailhead, Kokee Park, Kauai.

Dubautia latifolia (A. Gray) Keck—*BGB 675*, (*Flynn 1209*[2]), Makaha Ridge, Kokee Park, Kauai.

Dubautia laxa Hook. & Arn. subsp. *hirsuta* (Hillebrand) G. Carr—(*GDC 833*[3]a, b) (P), Mt. Kaala, Waianae Range, Oahu; (*Flynn 3201*[4]) (P), Pihea Trail, Alakai Swamp, Kauai.

Dubautia laxa Hook. & Arn. subsp. *laxa*—*BGB 662*, Pu'u Kukui, West Maui.

TABLE 1. Continued.

Dubautia linearis (Gaudich.) Keck subsp. *hillebrandii* (H. Mann) G. Carr—*BGB 531* (P), Pohakuloa Military Reservation, Hawaii.

Dubautia linearis (Gaudich.) Keck subsp. *linearis*—(*BGB 516*) (P), Piilani Highway E of Ulupalakua, East Maui.

Dubautia menziesii (A. Gray) Keck—*BGB 522* (P), (*BGB 521*) (P), west slope of Haleakala, East Maui.

Dubautia microcephala Skottsb.—*GDC 1044*[1]a (b) (P), Kahuamaa Flat, Kokee Park, Kauai; (*BGB 671*), Kaluapuhi Trailhead, Kokee Park, Kauai.

Dubautia paleata A. Gray—*GDC 1375*c (a, b, d) (P), Pihea Trail, Alakai Swamp, Kauai.

Dubautia pauciflorula H. St. John & G. Carr—*BGB 668*, Wahiawa Mountains, Kauai.

Dubautia plantaginea Gaudich. subsp. *humilus*—(*GDC 1183*), Black Gorge, West Maui.

Dubautia plantaginea Gaudich. subsp. *plantaginea*—*GDC 1180*, Castle Trail, Koolau Range, Oahu; (*GDC 838*[5]a, b, c) (P), Mt. Kaala, Waianae Range, Oahu.

Dubautia platyphylla (A. Gray) Keck—*BGB 524*, (*BGB 523*) (P), west slope of Haleakala, East Maui.

Dubautia raillardioides Hillebrand—*BGB 670* (P), border of Wahiawa Bog, Kauai; (*GDC 1373*a, b, c) (P), Pihea Trail, Alakai Swamp, Kauai.

Dubautia reticulata (Sherff) Keck—*BGB 664*, Koolau Gap, Haleakala Crater, East Maui.

Dubautia scabra (DC.) Keck subsp. *scabra*—*BGB 530* (P), Crater Rim Trail, Kilauea, Hawaii; (*BGB 526*) (P), near Pu'u Huluhulu, Hawaii.

Dubautia sherffiana Fosb.—*BGB 515* (P), Kamaileunu Ridge, Waianae Range, Oahu; (*GDC 837*a, b, c, d) (P), Mt. Kaala, Waianae Range, Oahu.

Madia bolanderi (A. Gray) A. Gray—*BGB 509*, Lake Tahoe, Sierra Nevada, California.

Raillardiopsis muirii (A. Gray) Rydb.—*BGB 618* (P), Santa Lucia Range, California.

Wilkesia gymnoxiphium A. Gray—*Char 76.022*c (a, b) (P), Iliau Loop Trail, Waimea Canyon rim, Kauai; (*GDC 1157*a, b, c) (P), Waimea Canyon Rd., Kauai.

Wilkesia hobdyi H. St. John—*GDC 1150*, Polihale Ridge, Kauai.

lutions was created using the PAUP CONTREE program. Confidence intervals were derived for each resolved node of the consensus tree using the same data matrix and the PHYLIP statistical package, version 3.1 (J. Felsenstein, Univ. of Washington) bootstrap (BOOT) option (100 replicate runs). Dollo parsimony analysis was conducted with the PHYLIP DOLLOP program from a similar data matrix that indicated double and single fragment profiles for each mutation.

We conducted two genetic distance analyses of

the restriction enzyme data. Chloroplast DNA divergence values (p values) for all pairwise species combinations were calculated from restriction site variation following Nei & Li (1979). These estimates of nucleotide substitutions per nucleotide position were used to produce (1) a Fitch & Margoliash (1967) dendrogram (FITCH program of PHYLIP) and (2) a phenetic tree, from a modification of the Fitch-Margoliash algorithm (KITSCH program of PHYLIP) that assumes clocklike evolution of nucleotide sequences.

A preliminary survey of intraspecific cpDNA variation was conducted based on results from the above analyses of one to two populations per species. Additional populations (Table 1) were screened for one or more restriction site mutation(s) unique to a given species in the primary analysis or, where no such mutations existed, for restriction sites most diagnostic for that taxon.

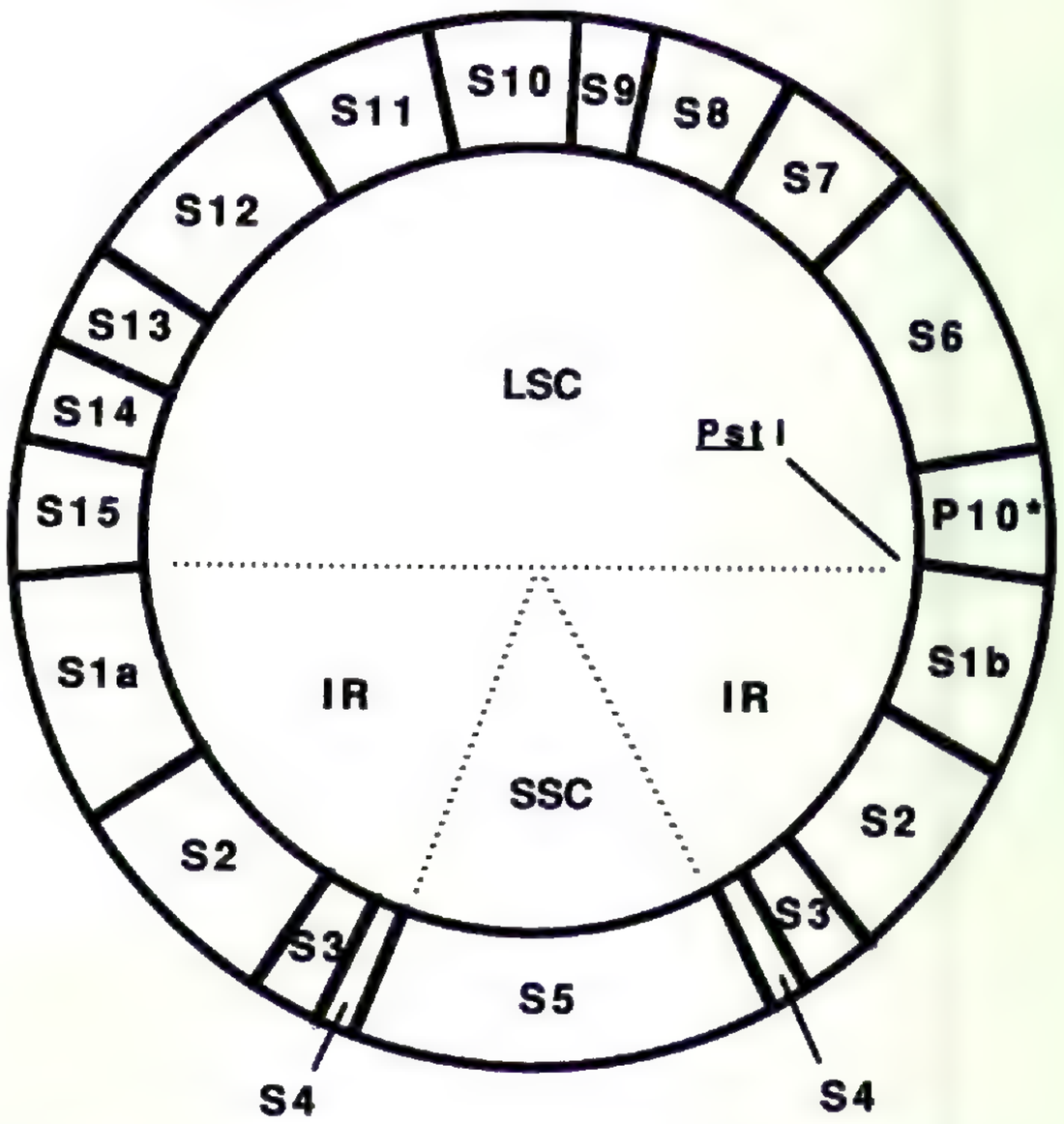

FIGURE 1. Molecular positions of cloned lettuce chloroplast DNA fragments (Jansen & Palmer, 1987) used as Southern blot hybridization probes. Unless otherwise indicated, all lines separating fragments are *Sac* I restriction sites. Fragments less than 1 kilobase in size are not indicated. Designations are: S = *Sac* I; P = *Pst* I; IR = inverted repeat; LSC = large single-copy region; SSC = small single-copy region. Sizes in kilobases of these fragments are: S1a = 12.3; S1b = 8.3; S2 = 9.9; S3 = 3.5; S4 = 1.8; S5 = 18.8; P10* = 7.1; S6 = 14.7; S7 = 7.0; S8 = 6.7; S9 = 3.8; S10 = 6.9; S11 = 7.7; S12 = 10.6; S13 = 4.6; S14 = 5.4; S15 = 6.3. Additionally, gel-isolated probes from digests of S6 (× *Kpn* I) and S12 (× *Xho* I) were used. "P10*" represents only that portion of the 9.0-kb *Pst* I *Petunia* fragment that bridges the inverted repeat and S6.

RESULTS

Approximately 875 restriction sites were examined in each cpDNA included in the main analysis. This accounted for 3.7% of the nucleotide sequence in each cpDNA. One of the two copies of the inverted-repeat cpDNA sequence was excluded from these estimates. Fifty-five restriction site differences were detected among the Hawaiian species, 36 (65.5%) of these being shared by a subset of two or more taxa (Table 2). Six additional mutations were common to all species of the silversword alliance and separated them from the two North American outgroup taxa.

Chloroplast DNA divergence within the silversword alliance ranged from 0 to 0.46% of nucleotides (p values; Table 3). For the samples used in the main restriction site analyses, complete interspecific identity in cpDNA was apparent in four instances: *Argyroxiphium caliginis/A. grayanum* (West Maui); *Dubautia imbricata/D. pauciflorula/D. raillardioides*; *D. ciliolata/D. scabra*; and *D. menziesii/D. platyphylla/D. reticulata*. Maximum cpDNA divergence was found within *Dubautia*, exceeding any intergeneric value among the Hawaiian species (Table 4). Genetic distances between the Kauaian rainforest shrub *Dubautia laevigata* and the Mauian bog rosette plants *Argyroxiphium caliginis* and *A. grayanum* (p = 0.15%) were the lowest of any intergeneric cpDNA comparisons, closely approaching the maximum divergence found within the genus *Argyroxiphium* (p = 0.13%), which is conservative in habit.

Chloroplast DNA restriction sites were most highly concentrated in the vicinity of the ribulose bisphosphate carboxylase, large-subunit gene (rbcL; S12) and near the inverted repeat-proximal end of the Compositae inversion (S6; Jansen & Palmer, 1987). Variation in both regions approached one mutation per kilobase (Table 5). Lower occurrences of mutations were found throughout the remainder of the large single-copy (LSC) and small single-copy (SSC; S5) regions (Fig. 1). Only two mutations clearly involved restriction sites within the inverted repeat (Fig. 1), in accord with its marked sequence conservation in other higher plant groups (Palmer & Zamir, 1982; Palmer et al., 1983a, b; Clegg et al., 1984; Sytsma & Gottlieb, 1986). Each of these two site differences yielded alternative fragment profiles with one common band and two others differing to the same extent in opposing digests (Table 2).

Intraspecific cpDNA variation was detected in eight of 15 species screened for specific site mutations found in the main analysis. The following samples lacked mutations unique to their species

TABLE 2. Restriction site mutations from ca. 875 restriction sites per cpDNA sampled in the primary analysis of Hawaiian Madiinae and two outgroup taxa (see Table 1). Mutations 1–43 were shared by a subset of two or more species (synapomorphies, including outgroup). The remaining site differences were unique to a single Hawaiian accession in the primary survey (autapomorphies). Mutations unique to the outgroup taxa are in Baldwin (1989). In three instances of outgroup conflict (mutations 9, 14, and 43) the derived condition has been designated based on the resolutions of Wagner and Dollo parsimony with the outgroups included. [1] No mutations were detected with *Hae* II, *Vsi* I, or *Sca* I. [2] The derived fragment condition (in kilobases) appears to the right of the hyphen, following the ancestral state. [3] See Figure 1 for molecular position. Uncertain location of a mutation is indicated by slashes (/) between regions. Hyphens (-) between regions indicate the common domain of both sequences. [4] 1 = *Raillardiopsis muirii*; 2 = *Madia bolanderi*; 3 = *Wilkesia gymnoxiphium*; 4 = *W. hobdyi*; 5 = *Dubautia knudsenii*; 6 = *D. imbricata*; 7 = *D. pauciflorula*; 8 = *D. raillardioides*; 9 = *D. paleata*; 10 = *Argyroxiphium sandwicense*; 11 = *A. grayanum* (E. Maui); 12 = *A. caliginis*; 13 = *A. grayanum* (W. Maui); 14 = *Dubautia plantaginea*; 15 = *D. laxa*; 16 = *D. scabra*; 17 = *D. ciliolata*; 18 = *D. linearis*; 19 = *D. arborea*; 20 = *D. menziesii*; 21 = *D. platyphylla*; 22 = *D. reticulata*; 23 = *D. herbstobatae*; 24 = *D. sherffiana*; 25 = *D. microcephala*; 26 = *D. laevigata*; 27 = *D. latifolia*. [5] Additional fragment profile from a single mutation occurring within the inverted repeat near the LSC borders.

Enzyme[1]	Site mutation[2]	Region[3]	Mutated cpDNA[4]
1. *Bgl*II	1.7 + 0.7–2.4	S13	3–27
2. *Bst*NI	2.8–1.7 + 1.1	S1	25–27
3. *Bst*NI	2.5 -2.1 + 0.4	S6	3–27
4. *Bst*NI	0.7 + 0.7–1.4	S11	3, 4
5. *Bst*NI	0.8 + 0.1–0.9	S12	25, 26
6. *Dra*I	1.1 + 0.7–1.8	P10-S6	14–24
7. *Dra*I	1.2 + 1.8–3.0	P10-S6	14–17
8. *Dra*I	1.2–0.7 + 0.5	P10-S6	3–9
9. *Dra*I	1.2 + 1.5–2.7	S6	2, 10
10. *Dra*I	1.5–1.1 + 0.4	S6	14, 27
11. *Dra*I	0.9 + 0.2–1.1	S7	5–9, 14
12. *Dra*I	2.5–2.4 + 0.1	S8	14 -24
13. *Dra*I	0.3 + 2.1–2.4	S15	10, 11, 14, 15
14. *Eco*RI	2.6–1.4 + 1.2	S6	1, 14–24
15. *Eco*RI	1.4 + 0.7–2.1	S6	14–24
16. *Eco*RI	2.6 + 2.4–5.0	S6	25, 26
17. *Eco*RI	4.4 + 2.2–6.6	S7	16–19
18. *Eco*RI	3.7–2.5 + 1.2	S12	3, 4
19. *Eco*RI	1.6–1.0 + 0.6	S13	12–15
20. *Eco*RI	1.4 + 1.1–2.5	S5	25, 26
21. *Eco*RV	1.0 + 7.5–8.5	S7	16–19
22. *Eco*RV	7.5–4.2 + 3.3	S8	12, 13
23. *Eco*RV	4.9–4.5 + 0.4	S12/S13	3–27
24. *Hin*cII	2.4 + 4.4–6.8	S11	5–9
25. *Hin*dIII	1.6 + 1.0–2.6	S7/8	3–27
26. *Hin*dIII	4.5 + 6.6–11.1	S12	14–24
27. *Hpa*II	3.6 + 0.3–3.9	S5	5–9
28. *Hpa*II	1.0 + 1.0–2.0	S6	3–27
29. *Hpa*II	0.4 + 0.5–0.9	S10	14, 15
30. *Hph*I	1.7 + 1.5–3.2	S6	14–24
31. *Hph*I	3.9 + 0.9 4.8	S8	23, 24
32. *Hph*I	1.1 + 0.7–1.8	S12	16, 17
33. *Ssp*I	1.9 + 1.0–2.9	S1	5–9, 27
34. *Ssp*I	4.0 + 0.1 4.1	S1	16 -22
35. *Ssp*I	3.8–3.6 + 0.2	S3/4/5	3–9
36. *Ssp*I	0.4 + 0.4–0.8	P10-S6	3–27
37. *Ssp*I	1.2–1.0 + 0.2	S6	5–8
38. *Xba*I	32.5 + 6.7–39.2	S5	25–27
39. *Xba*I	2.8 + 2.4–5.2	P10	5–9, 19
40. *Xba*I	2.3–1.3 + 1.0	S6	20–22
41. *Xba*I	2.3 + 1.5–3.8	S12	5–9

TABLE 2. Continued.

Enzyme[1]	Site mutation[2]	Region[3]	Mutated cpDNA[4]
42. *Xmn*I	0.5 + 1.3–1.8	S1	3–9
43. *Xmn*I	6.3 + 0.7–7.0 (4.9 + 0.7–5.6)[5]	S1	2, 3, 10, 20–22, 25
44. *Bgl*II	5.7–4.6 + 1.1	S5	25
45. *Bst*NI	1.8 + 0.8–2.6	S6	3
46. *Bst*NI	1.1 + 0.2–1.3	S9	19
47. *Bst*NI	1.1–1.0 + 0.1	S9	9
48. *Bst*NI	0.2 + 0.1–0.3	S12	4
49. *Dra*I	1.2 + 1.1–2.3	P10-S6	27
50. *Dra*I	3.1 + 0.5–3.6	S8	24
51. *Dra*I	8.2 + 0.7–8.9	S10	24
52. *Eco*RI	3.7–2.1 + 1.6	S12	5
53. *Eco*RI	0.9 + 0.2–1.1	S15	11
54. *Hpa*II	2.6–1.5 + 1.1	S12	4
55. *Hph*I	3.9–2.6 + 1.3	S5	4
56. *Nde*I	7.9–4.8 + 3.1	S6	10
57. *Nde*I	1.0 + 1.0–2.0	S14	24
58. *Ssp*I	0.9 + 1.3–2.2	S12	15
59. *Ssp*I	1.0–0.5 + 0.5	S12	27
60. *Xba*I	4.3 + 1.3–5.6	S12/S13	9
61. *Xmn*I	8.6–7.0 + 1.6 (7.9–6.3 + 1.6)[5]	S1	24

in the primary survey, most of these taxa being different subspecies than those analyzed in depth (number in parentheses = mutation designation in left column of Table 2): *Argyroxiphium sandwicense* subsp. *macrocephalum GDC 1239* (56); *Dubautia arborea BGB 656* (46); *D. laxa* subsp. *hirsuta GDC 833*a, b, *Flynn 3201* (58); *D. knudsenii* subsp. *filiformis GDC 1234* (52); *D. knudsenii* subsp. *nagatae GDC 1322*a, b (52); and *Wilkesia gymnoxiphium GDC 1157*a (45). The last sample of *W. gymnoxiphium*, however, indicates intrapopulational cpDNA variation in this taxon. In addition, populations of three species—again, mostly subspecies not sampled in the main analysis—lacked mutations shared between their species and one or more others in the primary survey: *Dubautia ciliolata* subsp. *glutinosa BGB 525, BGB 659* (21, 32); *D. linearis* subsp. *linearis BGB 516* (21); *D. plantaginea* subsp. *humilis GDC 1183* (6, 7, 10); and *D. plantaginea* subsp. *plantaginea GDC 838*a, b, c (10). No intraspecific cpDNA variation was observed in *Dubautia latifolia*, *D. menziesii*, *D. microcephala*, *D. paleata*, *D. platyphylla*, *D. raillardioides*, or *D. sherffiana*.

Four length polymorphisms resulting from insertions or deletions of ca. 50–250 nucleotides were resolved within the silversword alliance (Table 6). Three of these four mutations occurred in the LSC region near the inverted repeat (S1 and S6; Fig. 1), regions noted for high incidence of length variation in many plants (Palmer, 1985). The remaining mutation occurred in the SSC region (S5; Fig. 1). Smaller-length polymorphisms could not be well resolved by the gel-systems used. Involvement of the deletion shared by *Dubautia plantaginea* and *D. laxa* in an unscored *Ssp* I site loss in these species was inferred from diminished size of the resulting fragment. This length mutation was absent in the sole accession of *D. plantaginea* subsp. *humilis* (Table 1).

Wagner parsimony analysis of the entire data set (including outgroups) using the PAUP package branch-and-bound (BANDB) option found 1,035 maximally parsimonious trees at 53 steps. The high number of maximally parsimonious trees was attributable to arbitrary resolutions of zero-length branches by PAUP. A PAUP Wagner analysis of these data using the GLOBAL and MULPARS options also found minimum-length trees of 53 steps. Strict consensus trees from the upper limit of 100 trees retained in both PAUP analyses were topologically congruent. The common tree from both approaches is presented in Figure 2. A PAUP Wagner branch-and-bound analysis of the two fully resolved, Kauaian sublineages of this tree (i.e., *Wilkesia/Dubautia* sister group; *Dubautia laevigata/D. latifolia/D. microcephala*) indicated that each represented the most parsimonious topology. Wagner branch-and-bound analysis of the

TABLE 3. Pairwise cpDNA divergence among primary Hawaiian Madiinae samples and outgroup taxa (see Table 1). Values in the upper right half of matrix are numbers of mutations separating two cpDNAs from ca. 875 restriction sites sampled in each. Numbers of nucleotide substitutions per nucleotide position, or *p* values (Nei & Li, 1979), appear in the lower left half of matrix as 100*p*. Samples corresponding to the number designations along the left and top matrix borders are: 1 = *Raillardiopsis muirii*; 2 = *Madia bolanderi*; 3 = *Wilkesia gymnoxiphium*; 4 = *W. hobdyi*; 5 = *Dubautia knudsenii*; 6 = *D. imbricata/D. pauciflorula/D. raillardioides*; 7 = *D. paleata*; 8 =

	1	2	3	4	5	6	7	8	9	10
1	—	19	25	26	29	28	29	22	20	20
2	0.398	—	18	21	24	23	24	13	15	15
3	0.525	0.377	—	5	12	11	12	9	9	9
4	0.546	0.440	0.104	—	13	12	13	12	10	10
5	0.611	0.504	0.250	0.271	—	1	4	15	13	13
6	0.589	0.483	0.229	0.250	0.021	—	3	14	12	12
7	0.611	0.504	0.250	0.271	0.083	0.062	—	15	13	13
8	0.461	0.271	0.187	0.250	0.313	0.292	0.313	—	4	6
9	0.419	0.313	0.187	0.208	0.271	0.250	0.271	0.083	—	4
10	0.419	0.313	0.187	0.208	0.271	0.250	0.271	0.125	0.083	—
11	0.589	0.525	0.398	0.419	0.440	0.419	0.440	0.292	0.250	0.250
12	0.568	0.504	0.377	0.398	0.461	0.440	0.461	0.271	0.229	0.229
13	0.568	0.504	0.377	0.398	0.461	0.440	0.461	0.313	0.271	0.271
14	0.525	0.461	0.334	0.355	0.419	0.398	0.419	0.271	0.229	0.229
15	0.568	0.504	0.377	0.398	0.419	0.398	0.419	0.313	0.271	0.271
16	0.525	0.419	0.292	0.355	0.419	0.398	0.419	0.229	0.229	0.229
17	0.483	0.419	0.292	0.313	0.377	0.355	0.377	0.229	0.187	0.187
18	0.568	0.504	0.377	0.398	0.461	0.440	0.461	0.313	0.271	0.271
19	0.525	0.377	0.250	0.313	0.377	0.355	0.377	0.187	0.187	0.187
20	0.483	0.377	0.250	0.271	0.334	0.313	0.334	0.187	0.146	0.146
21	0.504	0.398	0.271	0.292	0.313	0.292	0.313	0.208	0.166	0.166

D. plantaginea/D. laxa/D. scabra/n = 13 *Dubautia* sublineage yielded nine maximally parsimonious resolutions, all concordant with the consensus topology. Bootstrap (PHYLIP BOOT program) confidence intervals for resolved consensus tree branches ranged from 59% to 100% (Fig. 2).

The consensus phylogeny, excluding the outgroups, had a consistency index (C.I.; Kluge & Farris, 1969) of 0.85 (15% parallelism) with 48 site losses and 24 site gains, including nine parallel losses and two parallel gains. Exclusion of two highly homoplasious characters (13 and 43; Table 2) resulted in the same consensus resolution with a C.I. of 0.91 (9% parallelism). These C.I. values include autapomorphies.

The high incidence of parallelism largely involved mutation "hotspot" centers at both ends of the LSC region, near the inverted repeat (Palmer, 1985). The predominance of parallelism involving the *Dubautia plantaginea* and *D. laxa* clade is not readily explained by length polymorphisms, introgression, or weak placement in the tree. Absence of a parallel site gain (10; Table 2) in additional populations of *D. plantaginea* suggests that this mutation indeed arose twice.

Dollo parsimony (PHYLIP package, DOLLOP program) analyses all yielded results topologically congruent with the strict consensus tree (Fig. 2). These trees, however: (1) consistently placed the *D. plantaginea/D. laxa* branch basal to *D. herbstobatae* and *D. sherffiana*, thereby resolving the *n* = 13 *Dubautia* species and *D. scabra* as a monophyletic group, and (2) placed *A. sandwicense* in a sister-group relationship with East Mauian *A. grayanum*.

Fitch-Margoliash genetic distance analysis yielded results completely harmonious with both the Wagner strict consensus tree (Fig. 2) and the Dollo parsimony results. The dendrogram produced was the best topology of all trees examined, i.e., in being most compatible with measured species divergences (Table 3). The average "standard deviation" of this outcome was 4.53%. Though fully resolved, this result was only slightly better than alternative conformations differing at nodes unresolved in the consensus tree. Accordingly, the entire dendrogram topology is not presented.

Phenetic analysis of the genetic distance values using the PHYLIP package, KITSCH program gave results contrary to the consensus tree (Fig. 2). Unlike all other analyses, the best phenetic resolution (average "standard deviation" = 26.06%) placed the following species, separated

TABLE 3. Extended.
Argyroxiphium sandwicense; 9 = *A. grayanum* (East Maui); 10 = *A. caliginis*/*A. grayanum* (West Maui); 11 = *Dubautia plantaginea*; 12 = *D. laxa*; 13 = *D. scabra*/*D. ciliolata*; 14 = *D. linearis*; 15 = *D. arborea*; 16 = *D. menziesii*/*D. platyphylla*/*D. reticulata*; 17 = *D. herbstobatae*; 18 = *D. sherffiana*; 19 = *D. microcephala*; 20 = *D. laevigata*; 21 = *D. latifolia*.

11	12	13	14	15	16	17	18	19	20	21
28	27	27	25	27	25	23	27	25	23	24
25	24	24	22	24	20	20	24	18	18	19
19	18	18	16	18	14	14	18	12	12	13
20	19	19	17	19	17	15	19	15	13	14
21	22	22	20	20	20	18	22	18	16	15
20	21	21	19	19	19	17	21	17	15	14
21	22	22	20	20	20	18	22	18	16	15
14	13	15	13	15	11	11	15	9	9	10
12	11	13	11	13	11	9	13	9	7	8
12	11	13	11	13	11	9	13	9	7	8
—	3	9	9	11	9	7	11	19	17	16
0.062	—	8	8	10	8	6	10	18	16	17
0.187	0.166	—	2	4	6	6	10	18	16	17
0.187	0.166	0.041	—	2	4	4	8	16	14	15
0.229	0.208	0.083	0.041	—	6	6	10	18	16	17
0.187	0.166	0.125	0.083	0.125	—	4	8	14	14	15
0.146	0.125	0.125	0.083	0.125	0.083	—	4	14	12	13
0.229	0.208	0.208	0.166	0.208	0.166	0.083	—	18	16	17
0.398	0.377	0.377	0.334	0.377	0.292	0.292	0.377	—	2	9
0.355	0.334	0.334	0.292	0.334	0.292	0.250	0.334	0.041	—	7
0.334	0.355	0.355	0.313	0.355	0.313	0.271	0.355	0.187	0.146	—

by slash marks, in sister-group relationships: (1) the species of *Argyroxiphium*/*Dubautia laevigata*; (2) *Dubautia menziesii*, *D. platyphylla*, *D. reticulata*/*D. sherffiana*; and (3) *Dubautia herbstobatae*/*D. arborea*, *D. ciliolata*, *D. linearis*, *D. scabra*.

DISCUSSION

CHLOROPLAST DNA DIVERGENCE

Chloroplast DNA nucleotide sequence divergence within the silversword alliance ($p = 0$–0.46%) was similar to that of the least divergent continental genera that have been documented; e.g., *Helianthus* ($p = 0.3\%$–0.4%; Rieseberg et al., 1988), *Lycopersicon* ($p = 0$–0.7%; Palmer & Zamir,

TABLE 4. Limits of intrageneric and intergeneric chloroplast DNA divergence detected in Hawaiian Madiinae. Divergence values (p = nucleotide substitutions per nucleotide position) are from Table 3.

	Minimum (p)	Maximum (p)
Argyroxiphium	0	0.13%
Dubautia	0	0.46%
Wilkesia	0.10%	0.10%
Argyroxiphium/*Dubautia*	0.15%	0.31%
Argyroxiphium/*Wilkesia*	0.19%	0.25%
Dubautia/*Wilkesia*	0.23%	0.42%
Total	0	0.46%

TABLE 5. Molecular distribution of chloroplast DNA restriction site mutations in Hawaiian Madiinae. Regions refer to probe sequences flanked by *Sac* I or *Pst* I restriction sites (see Fig. 1). [1] Region of the 9.0-kb *Pst* I sequence between the inverted repeat and S6. [2] Underestimated owing to unscored *Dra* I mutations not well resolved with S5 probe.

Regions	Numbers of mutations	Mutations/kilobase
S6 (14.7 kb)	14	0.95
S12 (10.6 kb)	10–11	0.94–1.04
S8 (6.7 kb)	4	0.60
S9 (3.8 kb)	2	0.53
S1 (12.3 kb)	6	0.49
S7 (7.0 kb)	3	0.43
S15 (6.3 kb)	2	0.32
S10 (6.9 kb)	2	0.29
S5 (18.8 kb)	5–6	0.27–0.32[2]
S11 (7.7 kb)	2	0.26
S13 (4.6 kb)	1–2	0.22–0.44
P10[1] (7.1 kb)	1	0.14

TABLE 6. Chloroplast DNA length mutations within the silversword alliance. Additional insertions and deletions smaller than 100 nucleotide pairs were not clearly resolved using the gel system employed. [1] Samples from the primary restriction site analysis (Table 1). [2] See Figure 1. [3] Direction of mutation based on outgroup comparison. [4] Same approximate map position but visibly larger insertion in *D. herbstobatae* relative to *D. sherffiana*.

Taxon[1]	Region[2]	Type of mutation[3]	Size of mutation
D. plantaginea			
D. laxa	S1	deletion	100–250 bp
D. paleata	S5	insertion	50–150 bp
D. herbstobatae[4]	P10/S6	insertion	50–100 bp
D. sherffiana[4]	P10/S6	insertion	50–100 bp

1982), *Lisianthius* ($p = 0$–0.3%; Sytsma & Schaal, 1985), and *Pennisetum* ($p = 0$–0.6%; Clegg et al., 1984). Overall allozymic variation among Hawaiian Madiinae also approximated that of some continental genera (Witter & Carr, 1988). Both measures of genetic differentiation, however, indicate higher levels of molecular divergence in the silversword alliance than in previously investigated autochthonous oceanic plant groups. For example, preliminary surveys of cpDNA variation in Hawaiian *Tetramolopium* (Asteraceae) and *Dendroseris* (Asteraceae) from the Juan Fernandez Islands revealed no polymorphism (Crawford et al., 1987), though fewer species and restriction sites were examined than in the present study.

Comparisons of cpDNA divergence values presented here with those measured among North American Madiinae (Baldwin, 1989) revealed expected and surprising patterns. Higher overall levels of divergence were found among the continental perennial taxa relative to within the silversword alliance. This accords with evidence indicating the mainland group is ancestral to the Hawaiian species (Baldwin, 1989). Maximum cpDNA divergence within *Dubautia* ($p = 0.46\%$), however, was similar to that between both North American outgroup species in this study (*Madia bolanderi* and *Raillardiopsis muirii*) and Hawaiian Madiinae. In fact, cpDNA genetic distances between North American *Madia bolanderi* and species of *Argyroxiphium* ($p = 0.27\%$–0.31%) were considerably less than in some comparisons within *Dubautia* (Table 7). These results suggest closer relationship of North American Madiinae to the silversword alliance than indicated by phenotypic considerations.

Patterns of sequence divergence in the silversword alliance (Fig. 2) suggest that cpDNA evolution has been irregular in this group. Conflicting results from the two genetic distance programs FITCH and KITSCH indeed provide evidence against operation of a cpDNA molecular clock among these species. In particular, lack of cpDNA sequence divergence was apparent in *Argyroxiphium*, comprising the silverswords and greenswords. Allozymic divergence within *Argyroxiphium* was likewise low (Witter, 1986). The mechanics of cpDNA evolution are still too little understood (Birky, 1988) to address the lack of cpDNA divergence in *Argyroxiphium*, i.e., does highly irregular or long-delayed sexual reproduction in this genus influence the rate of cpDNA evolution?

COMPREHENSIVE PATTERN OF ADAPTIVE RADIATION

Origin of the silversword alliance from a single colonizing event to the Hawaiian archipelago, or at most a few events closely spaced in time, is strongly suggested by the high confidence (89%) that this group is monophyletic (Fig. 2). This is completely concordant with the interfertility and cytogenetic cohesiveness of these species. Further, the basal, unresolved hexachotomy of the consensus tree is consistent with a rapid radiation of major lineages early in the history of the alliance. This pattern could alternatively be explained by an increase in the rate of cpDNA evolution through time or a period of extensive hybridization and introgression that led to fixation of one cpDNA type throughout Hawaiian Madiinae. The wealth of systematic data for the silversword alliance, however, supports close genetic affinities among all members despite extreme phenotypic and ecological differences, exactly as would be expected in a group that underwent explosive diversification. This explanation has also been proposed for similar unresolved cpDNA polychotomies among sections of *Clarkia* (Sytsma & Smith, 1988) and in Oncidiinae (reviewed in Palmer et al., 1988).

BIOGEOGRAPHIC CONSIDERATIONS

A consistent feature of the cpDNA consensus tree topology is the strong positive correlation between species affinity and geographic proximity. In almost every case where resolution was available, individual species were most closely grouped with others occurring on the same island. This correlation suggests two hypotheses. First, this pattern alone suggests that few successful interisland colonizations led to subsequent species radiations. Second, extensive introgressive hybridization or hybrid

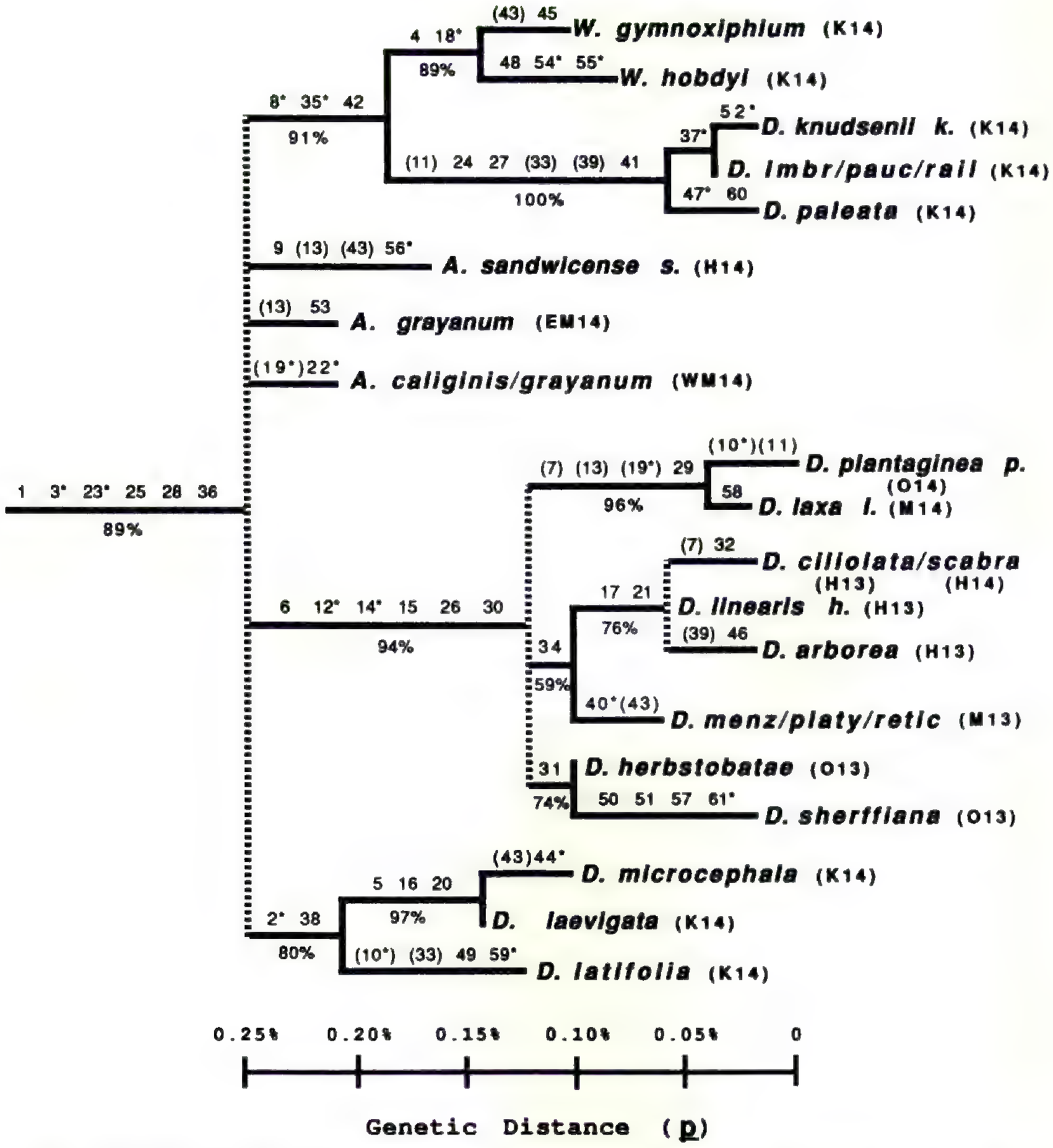

FIGURE 2. Strict consensus tree from Wagner parsimony analyses of a chloroplast DNA restriction site survey of Hawaiian Madiinae (see Table 1). Evolutionary polarity was determined by global parsimony using two North American tarweeds, *Madia bolanderi* and *Raillardiopsis muirii*. The best resolutions from Dollo parsimony and the Fitch-Margoliash genetic distance algorithm were congruent with this topology. Numbers above the horizontal branches refer to mutation designations in the left column of Table 2. Asterisks (*) denote restriction site gains; parentheses ( ) enclose characters showing evolutionary parallelism or homoplasy. This parallelism accounts for slight deviation between genetic distances (p) here and those in Table 3. Bootstrap confidence intervals are given below the horizontal branches as percentages. Broken lines indicate unresolved polychotomies. Taxon abbreviations are: *A.* = *Argyroxiphium*; *D.* = *Dubautia*; *W.* = *Wilkesia*; *D. imb/pauc/rail* = *Dubautia imbricata*, *D. pauciflorula*, and *D. raillardioides*; *D. menz/platy/retic* = *Dubautia menziesii*, *D. platyphylla*, and *D. reticulata*. See Table 1 for additional species data. Abbreviations following taxa names give the island of sample origin followed by the haploid chromosome number: K = Kauai; O = Oahu; M = Maui; EM = East Maui; WM = West Maui; H = Hawaii (Big Island). Only five species (*A. sandwicense*, *D. laxa*, *D. linearis*, *D. plantaginea*, *D. scabra*) have known distributions on multiple islands (Carr, 1985).

speciation on a given island may have resulted in the observed cpDNA relationships. The most widespread species in the alliance, *Dubautia plantaginea* and *D. laxa*, found on most of the Hawaiian Islands, are important for assessing these hypotheses. On different islands these species could be introgressed with or ancestral to local endemics. The consensus tree topology (Fig. 2) does not preclude one of these two taxa from being an old, genetically polymorphic species that founded existing lineages. Preliminary evidence of considerable intraspecific cpDNA variation between *D. plantaginea* on Maui and Oahu is therefore intriguing.

Another biogeographically interesting cpDNA pattern was resolved strictly among the *Dubautia* species having a chromosome number of $n = 13$ (hereafter "$n = 13$ *Dubautia*"). Carr & Kyhos (1986) argued from cytology, morphology, and distribution that these species form a monophyletic assemblage derived from an ancestral $n = 14$ *Dubautia* genome by a single reciprocal translocation followed by dysploidy. Close relationship of all $n = 13$ *Dubautia* taxa is also evident from their

TABLE 7. Lowest chloroplast DNA divergence values between silversword alliance species and the North American tarweed outgroup taxa, *Madia bolanderi* and *Raillardiopsis muirii*. These genetic distances (*p* values, Table 3) are equivalent to or actually exceeded by some among Hawaiian Madiinae.

Divergence from *Madia bolanderi* (*p*)		Divergence from *Raillardiopsis muirii* (*p*)	
Argyroxiphium sandwicense	0.27%	*Argyroxiphium caliginis*	0.42%
Argyroxiphium caliginis	0.31%	*Argyroxiphium grayanum*	0.42%
Argyroxiphium grayanum	0.31%	*Argyroxiphium sandwicense*	0.46%
Wilkesia gymnoxiphium	0.38%		
Dubautia laevigata	0.38%		
Dubautia microcephala	0.38%		
Dubautia latifolia	0.40%		
Dubautia reticulata	0.42%		
Dubautia menziesii	0.42%		
Dubautia platyphylla	0.42%		
Dubautia herbstobatae	0.42%		
Wilkesia hobdyi	0.44%		
Dubautia linearis	0.46%		

average identity in allozymes, comparable to that of a single mainland species (Witter & Carr, 1988). Accordingly, except for the position of *D. scabra* (see below), all Dollo parsimony analyses of the cpDNA data resolved $n = 13$ *Dubautia* as monophyletic. Aside from the basal phylogenetic ambiguity, the cpDNA consensus tree (Fig. 2) is similarly consistent with monophylesis of $n = 13$ *Dubautia*.

A unidirectional, west-to-east pattern of colonization from Oahu to progressively younger islands by members of the $n = 13$ *Dubautia* lineage is suggested by cpDNA phylogenetic data (Fig. 2), albeit with limited statistical confidence from bootstrap analysis. This migratory trend was proposed for the silversword alliance in general by Carr et al. (1989) and is supported by allozymic data at the intraspecific level in some *Dubautia* taxa (Witter, 1986). The same pattern of migration was inferred from polytene chromosome analysis in Hawaiian picture-winged *Drosophila* (Carson, 1983).

Instances of back-migration from younger to older islands cannot, however, be dismissed for $n = 13$ *Dubautia*. Hybridization between such immigrants and established $n = 13$ species could result in fixation of a native cpDNA genome in the alien taxon. Natural interspecific hybridization among $n = 13$ *Dubautia*, resulting in highly fertile hybrids, has been documented for eight species combinations (Carr, 1985). Comparisons of phylogenies based on biparentally and uniparentally inherited characters are critical to understanding the influence of hybridization on these species. Allozymic (Witter, 1986; Witter & Carr, 1988) and cpDNA data both indicated monophylesis of the two Oahu $n = 13$ species, *D. herbstobatae* and *D. sherffiana*, but differed slightly in resolution of Mauian and Hawaiian $n = 13$ *Dubautia* relationships. *Dubautia linearis* subsp. *hillebrandei* was placed with *D. arborea* and *D. ciliolata* in the cpDNA consensus tree (Fig. 2) but was excluded from the allozyme-defined clade comprising *D. arborea*, *D. ciliolata*, *D. menziesii*, and *D. platyphylla*. This conflict could indicate that the cpDNA of *D. linearis* subsp. *hillebrandei* was obtained from another Hawaiian *Dubautia* taxon by hybridization. Such hybridization may explain (1) extreme disparity in flavonoids between *D. linearis* subsp. *hillebrandei* on Hawaii and subsp. *linearis* on Maui (W. J. Crins and B. A. Bohm, pers. comm.) and (2) anatomical similarities of *D. linearis* subsp. *hillebrandei* to *D. arborea* (Carlquist, 1959a). Intraspecific cpDNA polymorphism within $n = 13$ *Dubautia* species, including *D. linearis*, lends promise that additional sampling and cpDNA analyses accompanied by nuclear DNA studies will enhance resolution of biogeographic relationships and hybridization among these species.

PHYLOGENETIC IMPLICATIONS

1. *Wilkesia* and Kauaian *Dubautia*

A well-resolved cpDNA sublineage within the silversword alliance supports monophylesis of *Wilkesia* and of five Kauaian *Dubautia* species (*D. knudsenii*, *D. imbricata*, *D. paleata*, *D. pauciflorula*, and *D. raillardioides*). *Wilkesia* is also delimited by unique alleles and high identities in allozymes (Witter, 1986; Witter & Carr, 1988). Among Kauaian *Dubautia*, distribution of unique allozymes suggests close relationship between *D.*

knudsenii and *D. pauciflorula* and between *D. paleata* and *D. raillardioides* (Witter & Carr, 1988).

Surprisingly, *Wilkesia* and the above *Dubautia* species together comprise a single lineage. Both species in *Wilkesia*, *W. gymnoxiphium* and *W. hobdyi*, have large, yuccalike rosettes born on narrow, naked stems. Leaf venation in *W. gymnoxiphium* closely approximates the parallel-vein condition seen in many monocots (Carlquist, 1959a; Kim, 1987). Unlike these unusual Kauaian xerophytes, members of the cpDNA sister group of *Wilkesia* comprise a *Dubautia* lineage of Kauaian rainforest trees and shrubs having relatively typical dicot habits and leaf venation. The extensive phenotypic contrasts between these two groups were reviewed by Carr (1985). Close cpDNA affinity between *Wilkesia* and these *Dubautia* species represents a striking example of inconsistency between relative rates of cpDNA and phenotypic evolution. The taxonomic implication of this finding is that *Dubautia* is either paraphyletic (i.e., *Wilkesia* is derived from *Dubautia*) or polyphyletic, assuming that ancient hybridization does not account for this cpDNA pattern. The distribution of genome 1 species in *Dubautia* (discussed below), however, argues against polyphylesis of this genus (Carr & Kyhos, 1986).

The other lineage of endemic Kauaian *Dubautia* taxa, comprising *D. latifolia*, *D. laevigata*, and *D. microcephala*, is well delineated by two basal restriction site gains. These rainforest species are to varying degrees sympatric with members of the previous *Dubautia* group. This resolution places *D. latifolia*, the only liana in the silversword alliance, in close relationship with *D. laevigata*, a large shrub, and *D. microcephala*, a small tree.

II. *Argyroxiphium*

Resolved patterns of cpDNA relationship within *Argyroxiphium* (silverswords and greenswords) strongly suggest that either hybridization has been an active force in this genus or extreme evolutionary parallelism in morphology or cpDNA has occurred. These data place a bog greensword (*A. grayanum*) from West Maui in closer relationship to the sympatric bog silversword *A. caliginis* than to a presumably conspecific greensword on East Maui. In addition, a weaker cpDNA sister-species relationship between East Mauian *A. grayanum* and the parapatric silversword *A. sandwicense* was consistently resolved by Dollo, but not Wagner, parsimony.

Intergeneric hybrid origin of the allopatric and somewhat morphologically distinct greenswords on East and West Maui via different stabilized combinations of silversword and *Dubautia* species would account for these cpDNA patterns. This hypothesis is supported by the remarkably greensword-like appearance of the artificial F_1 hybrid *Argyroxiphium sandwicense* × *Dubautia plantaginea* (Carr & Kyhos, unpublished). The latter species occurs sympatrically with greenswords in both regions (Carr, 1985).

Alternatively, these cpDNA patterns may indicate extensive introgression resulting in movement of cpDNA from silversword to greensword or perhaps the reverse. Natural hybrids have been reported between *A. caliginis* and *A. grayanum* at Pu'u Kukui on West Maui (Carr, 1985), where these taxa were sampled. In addition, contact between *A. sandwicense* and *A. grayanum* on East Maui may have occurred until recently, prior to the decimation of these plants by feral mammals.

III. *Dubautia scabra* and $n = 13$ *Dubautia*

A compelling argument for introgressive cpDNA transfer can be made from the cpDNA relationship between *D. scabra* and $n = 13$ *Dubautia*. In contrast with incomplete cytogenetic knowledge of *Wilkesia*, *Argyroxiphium*, and Kauian *Dubautia* taxa, extensive chromosomal data indicate genomic uniformity among $n = 13$ *Dubautia* species (Carr & Kyhos, 1986). These last taxa appear to be derived from the $n = 14$ *D. scabra* by a reciprocal chromosomal translocation and can be linked through *D. scabra* to other $n = 14$ genomes. In addition, *D. scabra* and $n = 13$ *Dubautia* are markedly similar in morphology and distribution, reflected by their exclusive taxonomic segregation as *Dubautia* sect. *Railliardia*. This evidence suggests *D. scabra* is a likely sister taxon to $n = 13$ *Dubautia*. Terminal placement of *D. scabra* in the $n = 13$ *Dubautia* cpDNA lineage and cpDNA identity of *D. scabra* and *D. ciliolata* at Kilauea are therefore unexpected. If these cpDNA and cytogenetic results both reflect organismic phylogeny, one of two improbable scenarios must have occurred: (1) a centromere and two chromosome arms similar to those originally lost by the $n = 13$ group arose, concomitant with a reciprocal translocation, to re-create the $n = 14$ *D. scabra* genome by ascending dysploidy (i.e., *D. scabra* is derived from $n = 13$ *Dubautia*), or (2) multiple independent origins of the $n = 13$ genome occurred from *D. scabra* or a genomically identical progenitor (i.e., *D. scabra* or an immediate predecessor is ancestral to $n = 13$ *Dubautia*).

Field studies indicate that in nature *D. scabra*

hybridizes extensively with $n = 13$ *Dubautia* species to produce highly fertile F_1 generations (Carr, 1985). Six species combinations of this type are known. *Dubautia scabra* and *D. ciliolata* occur in sympatry in the two areas where the former was sampled. In addition to apparent F_1 hybrids occupying intermediate habitats at both sites, Crins et al. (1988) reported what appear to be introgressed flavonoid profiles from individuals at the Pu'u Huluhulu site. Uniformity of cpDNA between these species at Kilauea could have resulted from such introgression.

The unexpected cpDNA affinity of *D. scabra* ($n = 14$) to $n = 13$ *Dubautia* taxa may, however, be the result of earlier hybridization on Hawaii. Intraspecific variation between *D. ciliolata* subsp. *glutinosa* at Pu'u Huluhulu and *D. ciliolata* subsp. *ciliolata* at Kilauea is not mirrored by *D. scabra*, which is uniform at examined restriction sites in all of several plants from both localities. Chloroplast DNA transfer from *D. scabra* to *D. ciliolata* therefore appears a more likely explanation for this pattern than the reverse. In short, introgression may account for cpDNA identity between *D. scabra* and *D. ciliolata* at Kilauea, but would not account for $n = 13$ *Dubautia* cpDNA in *D. scabra*. The evolutionary history of these species is being further analyzed, in part, by examination of cpDNA from *D. scabra* on the older island Maui, where the Hawaiian $n = 13$ taxa *D. ciliolata*, *D. arborea*, and *D. linearis* subsp. *hillebrandei* do not occur.

IV. *Dubautia* genome 1

The distribution of *D. knudsenii*, *D. plantaginea*, *D. laxa*, and *D. microcephala* on the cpDNA tree conflicts with their common possession of genome 1 (Carr & Kyhos, 1986). Ancient and recent hybridization together could account for these discrepancies, i.e., cpDNA may not reflect phylogeny. It may be significant, however, that (1) cytogenetic variation within genome 1 species is imperfectly known, with sampling limited to single collections from one or two populations, and (2) these taxa are all found on the oldest Hawaiian island, Kauai, concordant with genomic antiquity.

The existence within individual species of two or more genome types differing by chromosomal rearrangements, a situation well documented in North American Madiinae (Clausen, 1951; Carr, 1975; Carr & Carr, 1983), could explain the cpDNA results. For example, *Dubautia plantaginea* and *D. laxa* are a minimum of two chromosomal interchanges removed from the group with which they showed cpDNA alliance and with which *D. plantaginea* had high genetic identity in allozymes (Witter & Carr, 1988): *D. scabra*/$n = 13$ *Dubautia*. A structurally intermediate genome in one of the first two species could explain evolutionary transition from genome 1 to the *D. scabra* genome. Although no intraspecific chromosomal variation is presently known from Hawaiian Madiinae, such undetected heterogeneity may account for unexpected cytogenetic results in *Argyroxiphium* (Carr & Kyhos, 1986). Expanded cpDNA investigations and molecular analyses of nuclear DNA are needed to clarify the relative extent to which hybridization, intraspecific differentiation, and evolutionary parallelism have influenced phylogenetic patterns in this remarkable group of plants.

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EVOLUTION IN THE MADIINAE: EVIDENCE FROM ENZYME ELECTROPHORESIS

Martha S. Witter[1]

ABSTRACT

The genetic differences observed among species contain historical information that is a function of their ancestry, mode of origin, and population structure over time. Studies of isozyme differentiation among the island species of *Dubautia*, *Wilkesia*, and *Argyroxiphium*, and among the mainland species of *Layia* are reviewed. Both groups provide examples of rapidly evolved progenitor-derivative species pairs as well as species showing gradual divergence as a function of their time of separation. A comparison of island and mainland taxa illustrates the effect of population structure on levels of genetic variability and the consequent effects on genetic differentiation among species. The colonization and speciation patterns within the Hawaiian archipelago can be inferred for some species pairs on the basis of shared unique alleles that are presumed to reflect a common ancestry. Gene duplications observed in the Madiinae suggest an ancient tetraploid origin for the Hawaiian species.

The Madiinae offer several advantages for the study of plant evolution. They are a cohesive, monophyletic group with a distinct biogeographic center of origin, the Pacific Coast of North America. The mainland genera inhabit most of the major community and habitat types within California. The Hawaiian genera have some of the most remarkably distinct morphologies found within the Compositae. Early work with the Madiinae included the classic studies of plant evolution done at the Carnegie Institution of Washington at Stanford (Clausen, 1962). *Layia* and *Madia* were used because they included species at various stages of evolutionary differentiation (Clausen, 1962). The Carnegie group worked on the assumption that the evolutionary record of a group of living species is reflected in the existing genetic relationships among species (Clausen, 1962). One of their primary means of assessing genetic relatedness was through experimental hybridization studies. Biochemical genetic techniques have provided new means of analyzing the number of genes shared by related species and have reduced the need to resort to time-consuming hybridization programs. Enzyme electrophoresis was the first technique that allowed the number of gene differences among species to be measured directly over a wide taxonomic range (Avise, 1974; Gottlieb, 1977). Modern molecular techniques promise to allow an even greater resolution of phylogenetic patterns and genetic divergence among species (Palmer, 1985). This paper will review the isozyme data available in the Madiinae to illustrate how the pattern and degree of genetic differentiation can be used to make inferences on the mode and tempo of genetic divergence among species.

GENETIC VARIATION AND GENETIC DIFFERENTIATION AMONG SPECIES: MAINLAND TAXA

In a study of the genus *Layia*, Clausen et al. (1941) used extensive analyses of morphological characters, cytogenetics, and fertility relationships from interspecific hybridizations. They found that one group of six species formed a complex consisting of three morphologically discontinuous groups: *L. platyglossa*; *L. fremontii* and *L. chrysanthemoides*; and *L. jonesii*, *L. leucopappa*, and *L. munzii* (Clausen et al., 1941; Clausen, 1962). They proposed that these species had arisen allopatrically, through the gradual accumulation of many small genetic changes as a result of differential selective pressures in different environments. The morphologically similar species represented more recent stages in the divergence and accumulation of genetic differences among taxa (Clausen, 1962).

The degree of genetic relatedness and the pattern of genetic divergence predicted by the model of allopatric evolution was tested using allozymes. Warwick & Gottlieb (1985) examined the species

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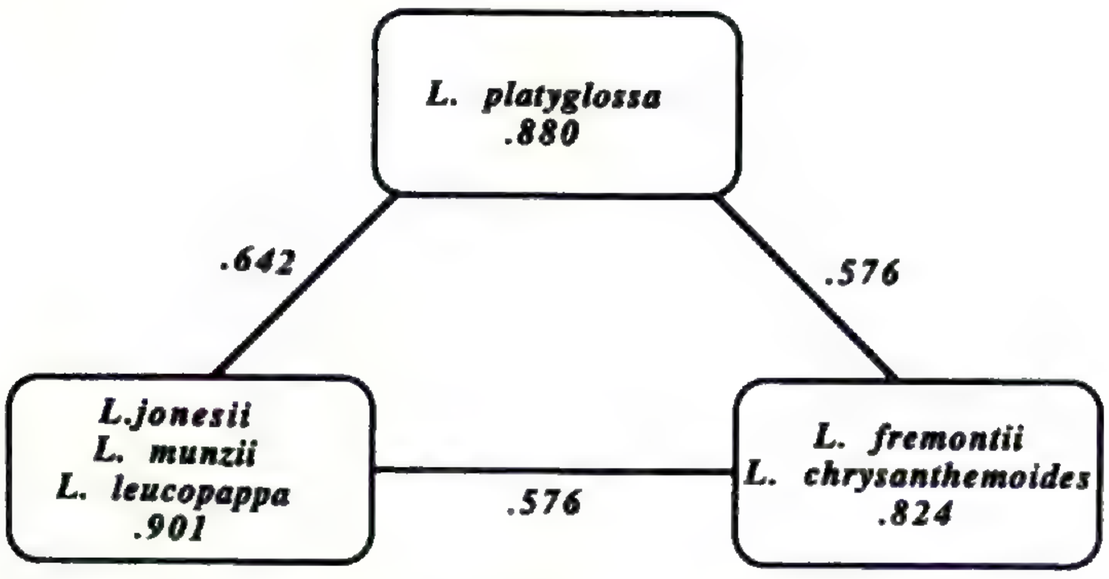


FIGURE 1. Summary of interpopulation and interspecific genetic identities (Nei, 1972) among the species of the *Layia platyglossa* complex. (Redrawn from Warwick & Gottlieb, 1985).

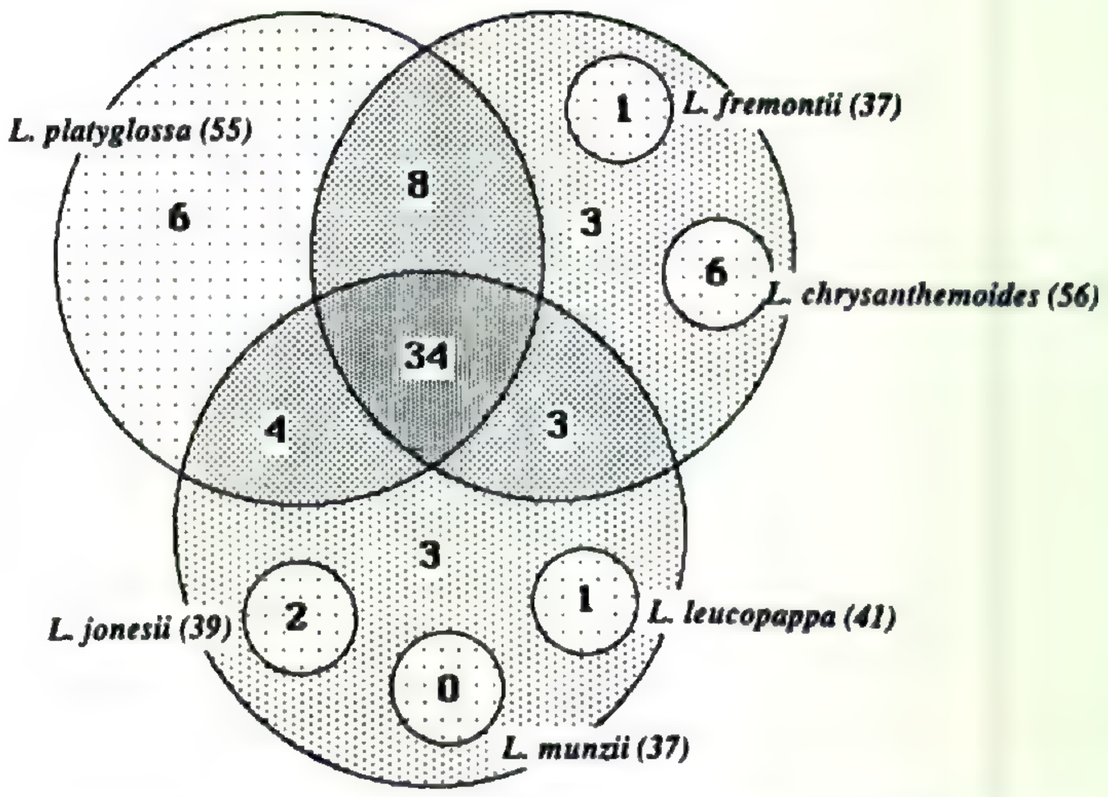


FIGURE 2. Numbers and distributions of individual alleles among the species of the *Layia platyglossa* complex. Total number of alleles identified per taxon is given in parentheses. Circles represent overlapping sets of individual species, individual species subgroups, and all three species subgroups of the complex. Numerals not in parentheses show the numbers of alleles that occur uniquely within individual species, within individual species subgroups, among any two subgroups, and the numbers of alleles that occur in all three subgroups (Gottlieb, unpublished data).

of the complex and found the genetic data to be fully concordant with an allopatric model of speciation (Fig. 1). Genetic distances were substantially higher among morphologically discontinuous species than among morphologically similar taxa. The pattern of allozymic divergence supports the concept of gradual genetic divergence through shifts in gene frequency. Figure 2 shows the distribution of alleles shared among taxa of the *L. platyglossa* complex. The vast majority of alleles are shared by either two or all three of the major species groups, while very few alleles are restricted to a single taxon or species group. All species of the complex are extremely polymorphic: an average of 67% of all loci are polymorphic per species, and the average number of alleles per locus is 3.4 (Warwick & Gottlieb, 1985). These data support the notion that allozymic divergence and genetic differentiation have occurred primarily as the result of changes in gene frequency from a rich, common pool of polymorphic gene loci. This pattern contrasts sharply with that observed in island populations.

ISLAND TAXA

The Hawaiian species of the Madiinae are renowned for their striking range of morphological and ecological diversification (Carr et al., 1988). The pattern of morphological and cytological differentiation is strongly correlated with the biogeographic distribution of species within the archipelago (Carr, 1978, 1985): many of the most morphologically specialized and differentiated species are endemic to the oldest island of Kauai and have the ancestral chromosome complement of 14 pairs of chromosomes. The cytologically most derived species, with 13 pairs of chromosomes, occur largely on the younger islands of Maui and Hawaii and are much less morphologically and cytologically differentiated than the Kauai endemics. Estimates of allozymic divergence agreed with the hypothesis that the Kauai species were ancestral to the 13-paired species and that the 13-paired species were of relatively recent origin (Fig. 3; Witter & Carr, 1988). As in previous studies of island endemics (Crawford et al., 1985; Helenurm & Ganders, 1985; Lowrey & Crawford, 1985), the 13-paired species had extremely high interspecific genetic identities, $I > 0.90$. The 14-paired taxa, however, were significantly differentiated, with values more

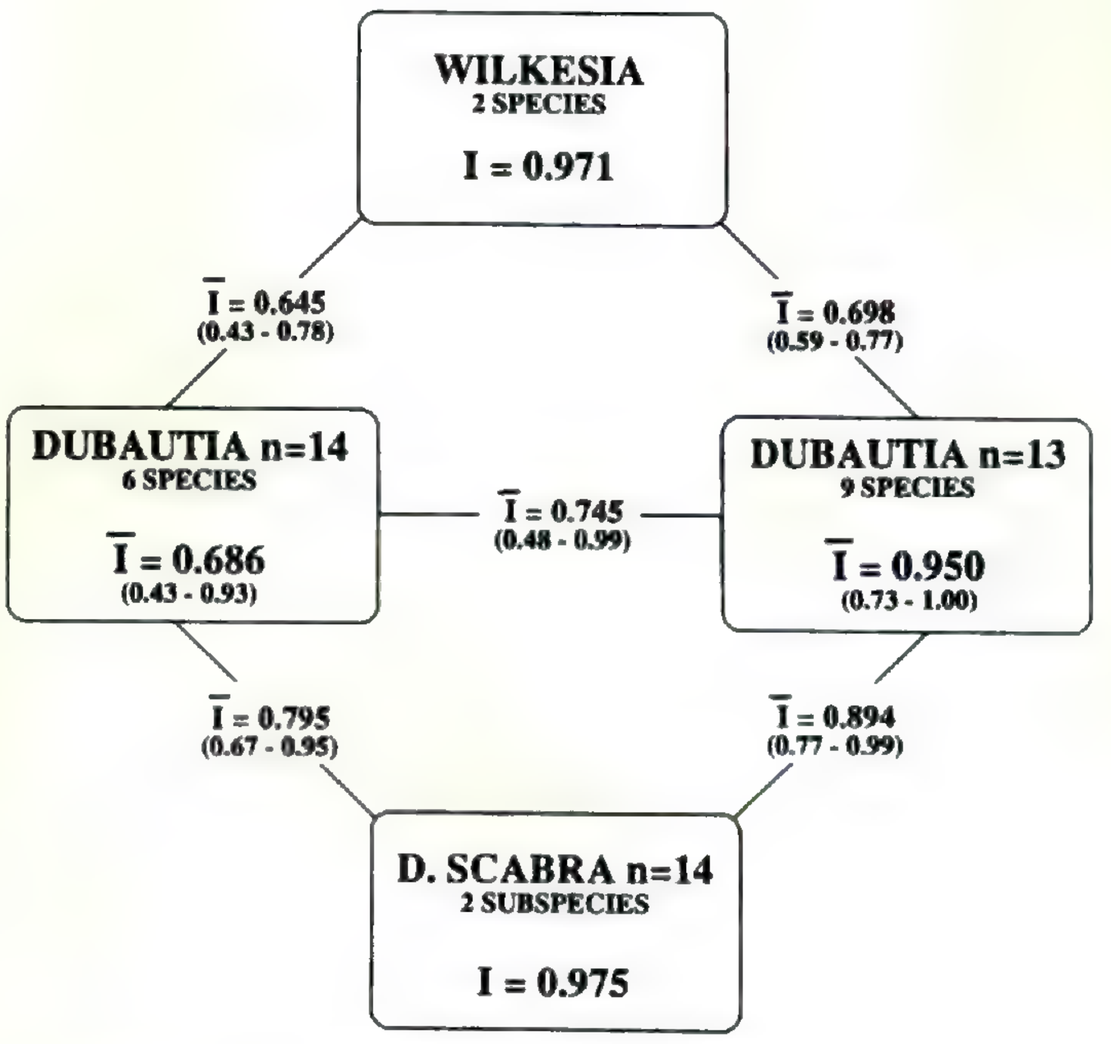


FIGURE 3. Summary of interspecific genetic identities (Nei, 1978) among the species of *Wilkesia* and *Dubautia*.

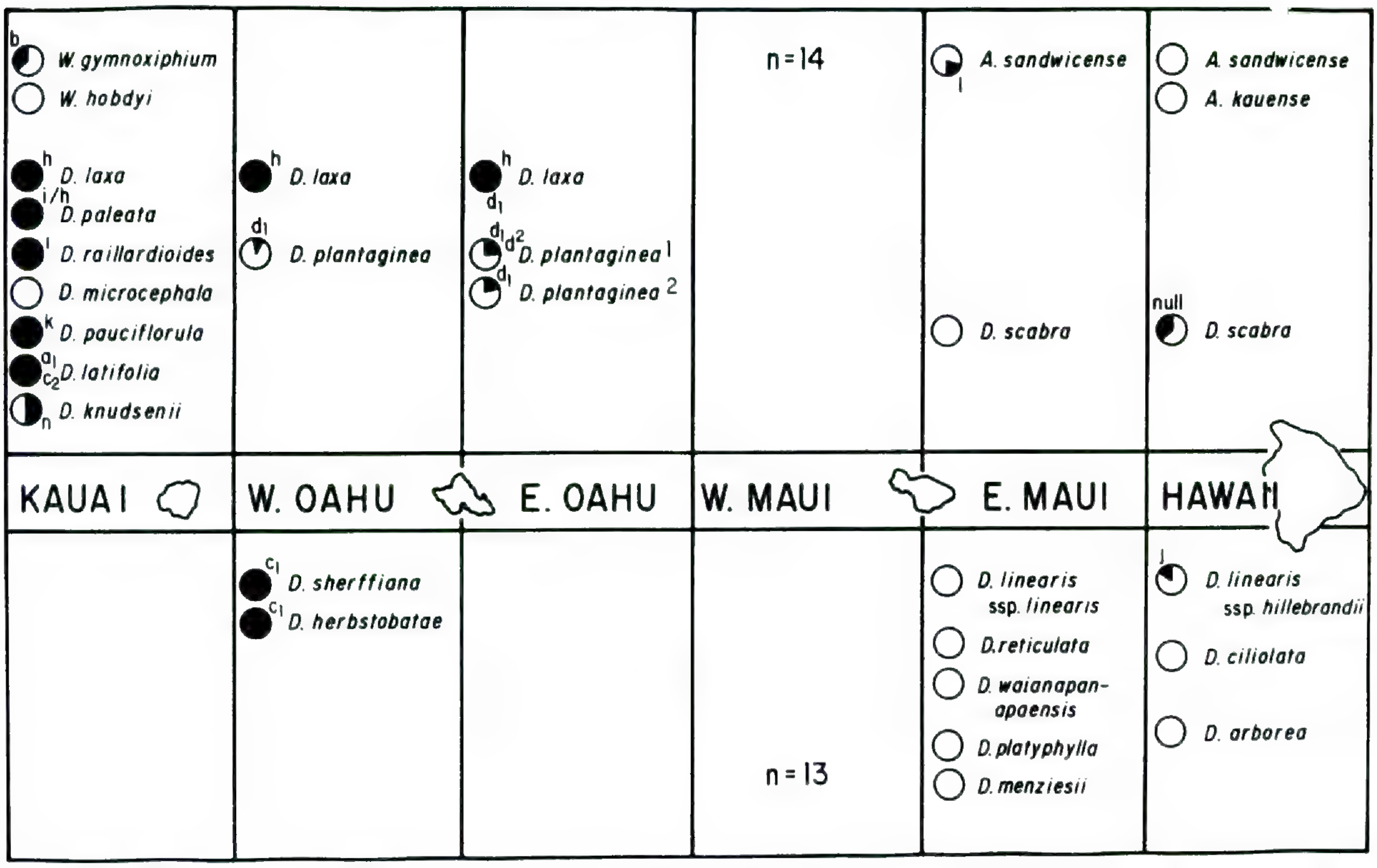


FIGURE 4. Distribution of allelic variants at the *Pgic 3* locus among the species of the Hawaiian Madiinae. The frequencies of particular alleles are illustrated in pie diagrams for each species. Open circles represent the frequency of a single, common allele that was found in a number of species. Closed circles represent the frequency of all other alleles found, most of which were restricted to one or two species.

typical of interspecific comparisons in other plant groups (I ~ 0.67, Gottlieb, 1981; Crawford, 1983). The results obtained for the 14-paired species of the Hawaiian Madiinae showed that insular plant populations do diverge genetically, but depend on sufficient lengths of time to accumulate genetic differences (Witter & Carr, 1988).

The pattern of interspecific genetic differentiation observed in island species appears to be the direct result of population structure. Low genetic variability in the Hawaiian Madiinae was attributed to founder events and genetic drift within small populations (Witter & Carr, 1988). Insular groups are frequently composed of small, localized populations with markedly decreased levels of genetic variation. For example, the Hawaiian Madiinae are approximately one-third as variable ($P = 0.24$, $A_1 = 1.29$) as the species of *Layia* discussed previously. Figure 4 illustrates the typical distribution of alleles at a single locus among the species of the Hawaiian Madiinae and can be used to make several points about the effect of genetic variability on genetic divergence within the Hawaiian Madiinae. A single, common allele usually predominates at each locus among most species, suggesting a genetically depauperate common ancestor. The low frequency of polymorphisms indicates that allozymic divergence will occur only as new mutants arise, rather than through gradual divergence in frequencies of multiple alleles at a given locus, as was observed in continental species of *Layia*. The distribution of alleles at *Pgic 3* (Fig. 4), for example, illustrates that the $n = 13$ species of *Dubautia* are all fixed for the same allele, which they presumably inherited from a single founder. The results of such a genetic bottleneck limit allozymic divergence among these taxa to the production and incorporation of new mutants. High genetic identities among the Hawaiian Madiinae are therefore not only a reflection of the length of time since divergence, but are also a function of the historical demography of species with consequent effects on genetic variability and structure of populations.

Progenitor-derivative Species Pairs

Harlan Lewis was the first to propose the revolutionary notion of saltational speciation in annuals, whereby a new species could arise rapidly and be reproductively isolated from its progenitor

through the fixation of structural chromosome rearrangements (Lewis, 1973). Gottlieb (1981), in one of the early and striking systematic applications of enzyme electrophoresis in plants, showed that a number of species pairs believed to be related as progenitor and derivative had very high genetic identities and that the derivative species possessed a less variable subset of the alleles present in the progenitor. Recently derived species have historically been of interest to evolutionary biologists for several reasons (Ayala et al., 1975; Gottlieb, 1973, 1974; Carson, 1976). Better inferences can often be made about the recent past than about the distant past. Where polarity between species pairs can be identified, the direction of evolution in character change can be studied. Recent species pairs are also often partially or fully compatible, and interspecific hybrids can be analyzed for the genetic basis of species differences.

Layia discoidea is a highly localized, morphologically unusual species. Its most obvious morphological characteristics are an absence of ray florets with their enclosing bracts and a reduction of the pappus. Originally believed to be an ancient relictual form because of its highly distinctive morphology, experimental hybridization showed it to be fully interfertile with *Layia glandulosa* (Clausen, 1962). Subsequent allozyme analysis indicated that *L. discoidea* was a recent derivative of *L. glandulosa* subsp. *lutea* (Gottlieb et al., 1985). Unlike other annual progenitor-derivative species pairs, *L. glandulosa* and *L. discoidea* are fully interfertile and freely recombining. With their distinct morphological characteristics, they are ideal for the study of the genetics of characters often used to separate taxa at higher taxonomic levels (Gottlieb et al., 1985; Ford & Gottlieb, 1989).

The Hawaiian taxa also have a number of species pairs that fit the criteria of recent progenitor and derivative. Both species of *Wilkesia* are endemic to the island of Kauai. *Wilkesia gymnoxiphium* is a monocarpic rosette plant on an elongated woody stalk up to 3 m at reproductive maturity. It is widespread along the upper margins and outer slopes of Waimea Canyon. *Wilkesia hobdyi* is much more restricted, known only from two populations on the sea cliffs of the Na Pali coast. Unlike *W. gymnoxiphium*, it is a multiply branched rosette plant which flowers repeatedly. The genetic identity between these two *Wilkesia* species is I = 0.971. At 8 out of 11 loci the two species share either identical monomorphic alleles or common polymorphisms, while at the remaining three loci *W. gymnoxiphium* is polymorphic and *W. hobdyi* possesses only one of the alleles of the polymorphism (Witter, 1986). *Wilkesia hobdyi* appears to be a recent derivative of the more widespread *W. gymnoxiphium* by the criterion of a reduced subset of genetic variability present in a derivative taxon. However, another possibility is that drift due to restricted population size could produce the decreased genetic variability in *W. hobdyi*. Even if evolutionary polarity for the changes remains unsettled, the two species of *Wilkesia* offer an ideal opportunity to study the origin, ecological dynamics, and genetics of the complex life history trait of monocarpy.

Although all members of the group of 13-paired species of *Dubautia* have high genetic identities (Fig. 3), *D. dolosa* and *D. reticulata* appear to be a good case of a progenitor-derivative species pair. *Dubautia reticulata* is a large tree in the rainforests of east Maui, whereas *D. dolosa* is a rainforest shrub. The two species have a Nei's I = 1.00, sharing the same alleles at all loci. Several unique alleles are found only in these two taxa, supporting their common divergence from the other 13-paired taxa (Fig. 5). As with the two species of *Wilkesia*, the polarity of the relationship cannot be established on the basis of these allozyme data. Again, however, these species offer unique experimental opportunities. The distinct differentiation of life form in two species with a similar genetic background can be used to examine the genetic basis of the complex character trait of life form. Ecological hypotheses to explain the adaptive nature of life form differences suggest that trees in a tropical wet forest have evolved in response to shading and competition for light, while shrub forms are often associated with nutritional or other stresses (Rundel, pers. comm.). *Dubautia reticulata* and *D. dolosa* can be used to test the functional basis of the adaptational differences between trees and shrubs in this habitat.

Duplicate Gene Expression

Duplicate gene expression can result either from duplication of a single locus or through polyploidization. Unlinked single gene duplications may have originated in plants heterozygous for overlapping reciprocal translocations and have a high probability of being unique phylogenetic markers of shared ancestry (Gottlieb, 1986). Gottlieb (1986) documented two such unlinked duplications in the Madiinae: the first is a PGM duplication found throughout the diploid mainland genera; the second is an IDH duplication found throughout *Layia* (Fig. 6). A second IDH duplication occurs in two species of *Layia* with a cytotype of $n = 8$, and may prove

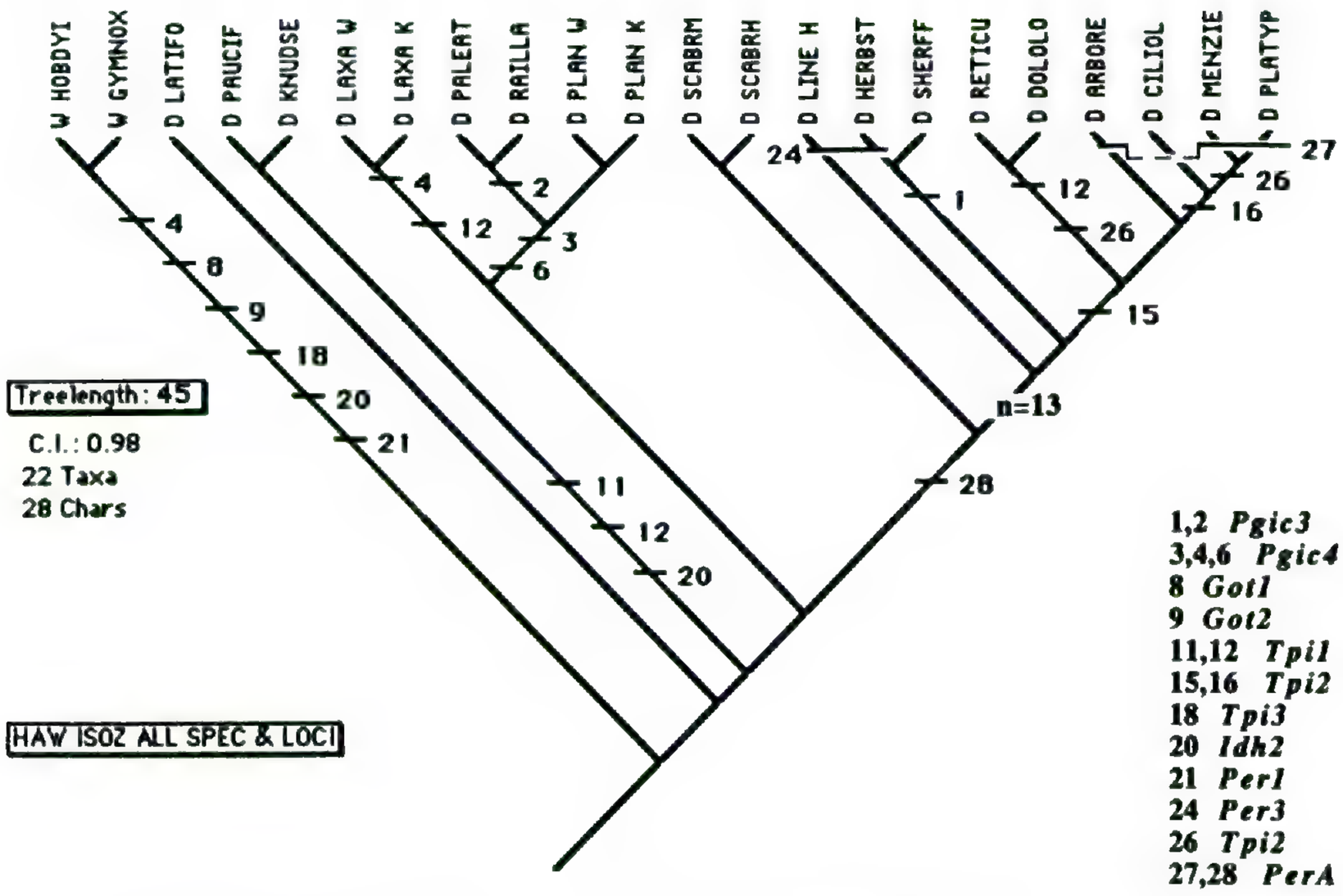


FIGURE 5. Distribution of unique alleles among the species of *Wilkesia* and *Dubautia*. The tree format was used to show the actual distribution of character states in the most consistent manner possible. The tree is arbitrarily rooted and polarity assumed and does not represent an actual phylogeny.

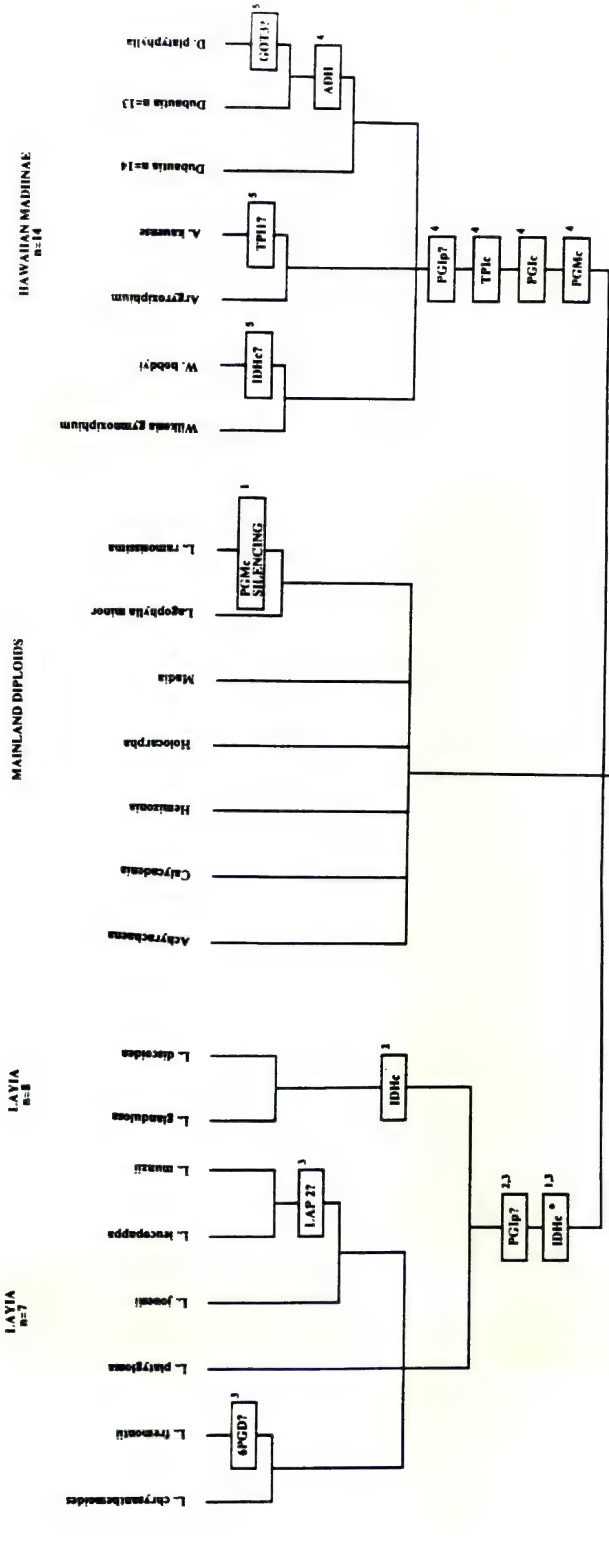
to be a phylogenetic marker for that section of *Layia* (Gottlieb et al., 1985; Fig. 6). Within *Layia* several other isozymic patterns are consistent with gene duplication, or could have arisen through other mechanisms, and must therefore be confirmed by genetic analysis. The LAP isozymes observed in the *Layia munzii* complex may be useful in resolving the trichotomy among the three taxa in this group (Fig. 6).

The Hawaiian Madiinae expressed three duplications in all taxa: PGMc, PGIc, and TPIc, and possibly a fourth locus, PGIp (Fig. 6). Because the base chromosome number in the Hawaiian Madiinae is $n = 14$, in a group where the ancestral condition is $n = 7$, it is assumed that these duplications result from polyploidization and are not multiple single gene duplications (Witter, 1988). This interpretation is supported additionally by the number of PGM loci expressed in the Hawaiian taxa. All Hawaiian species appear to express four PGM loci (Witter, 1988). The maximum number of expressed loci expected from an ancestral duplication in the Madiinae followed by polyploidization is four loci, the number observed. If the PGM loci were due to single gene duplications, it would be necessary to hypothesize two additional single gene duplications above the ancestral Madiinae PGM duplication.

The majority of 13-paired *Dubautia* species exhibited clear evidence of duplicated ADH activity, whereas there was no evidence of expressed duplications among the 14-paired species (Witter, 1988). The complex genetic model necessary to explain the pattern of phenotypic variation of ADH isozymes of the Hawaiian Madiinae needs further genetic analysis; however, the 13-paired species are clearly differentiated in their pattern of duplicated ADHs (Fig. 7), and these may be a useful phylogenetic marker among these species which are otherwise difficult to differentiate cytologically or isozymically. Most interesting is the differentiation of the three subspecies of *D. linearis*, the most widespread and variable of the 13-paired taxa.

Phylogenetic and Biogeographic Inferences From the Systematic Distribution of Unique Alleles in the Hawaiian Taxa

Argyroxiphium and *Wilkesia* each have a number of alleles that are unique to the genus and common to all taxa within the genus (Fig. 8). *Dubautia*, in contrast, has a large number of alleles unique to the genus, but these are largely restricted to single species or closely related species groups (Fig. 5). With the exception of a single PER phenotype common to *D. scabra* and the 13-paired species of *Dubautia*, and a single polymorphism, $Tpi2^a/Tpi2^d$, common to all lineages except *D. latifolia*, virtually no alleles define large clades within *Dubautia* (Figs. 5, 8). This suggests that some of the modern species of *Argyroxiphium* and *Wilkesia* are presumably much more recent than some of the lineages within *Dubautia*. In particular, the high genetic identity between the two


HAWAIIAN MADIINAE
n=14
D. platyphylla
GOT3?
Dubautia n=13
ADH
Dubautia n=14
A. kauense
TPI1?
Argyroxiphium
W. bobdyi
IDHc?
Wilkesia Zymoxiphium
L. ramosissima
PGMc SILENCING
Lagophylla minor
Madia
Holocarpha
Hemizonia
Calycadenia
Achyrachaena
PGIp?
TPIc
PGIc
PGMc
PGMc*
MAINLAND DIPLOIDS
LAYIA
n=8
L. glandulosa
L. discoidea
IDHc
LAYIA
n=7
L. chrysanthemoides
L. platyglossa
L. jonesii
L. leucopappa
L. muirii
L. glandulosa
L. discoidea
L. carnosa
L. minor
L. ramosissima
L. platyglossa
L. jonesii
L. leucopappa
L. muirii
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L. glandulosa
L. discoidea

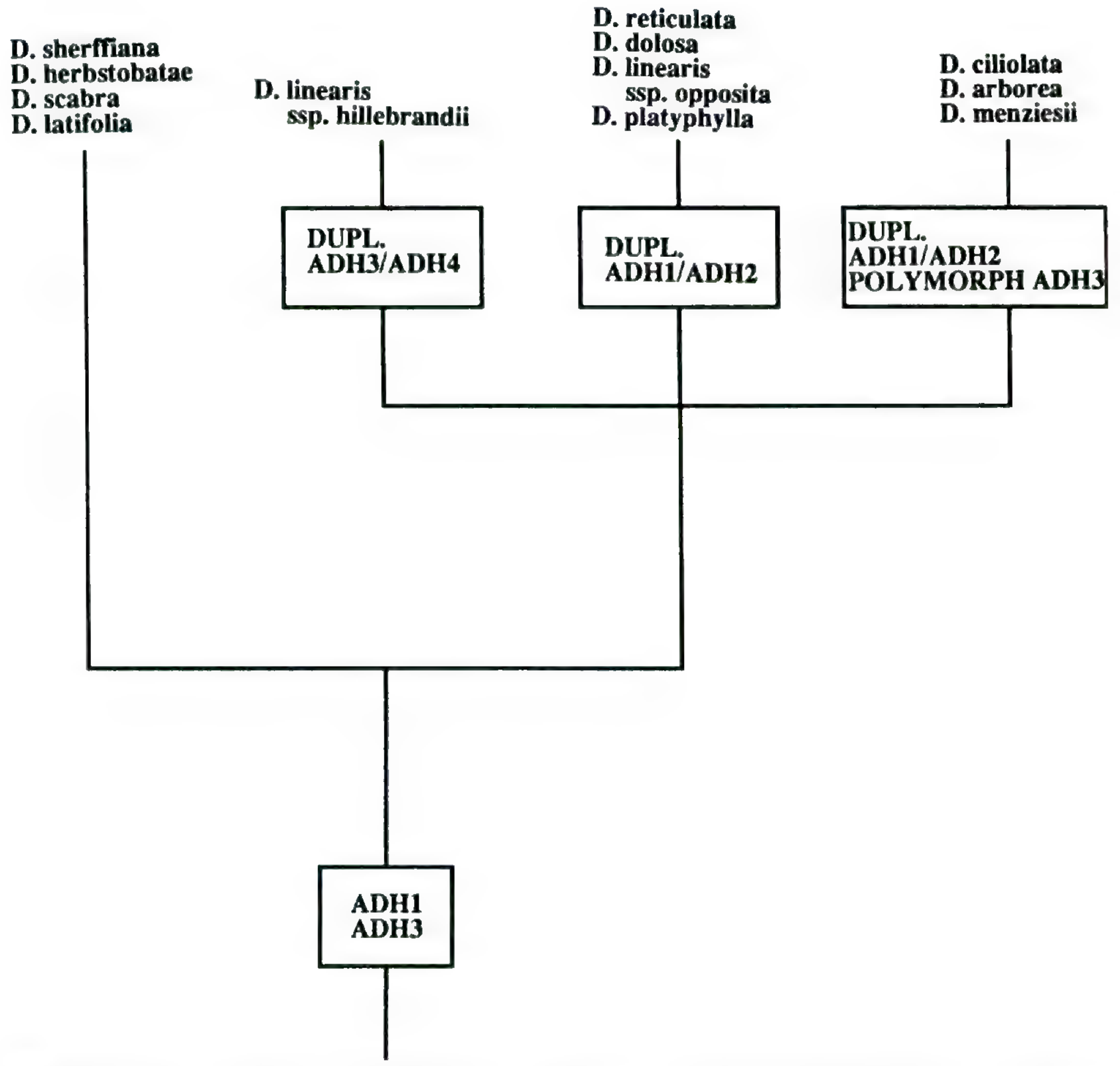

FIGURE 7. Differential expression of ADH isozymes among the species of *Dubautia* according to the genetic model of Witter (1988). All species are $n = 13$, except *D. latifolia* and *D. scabra*.

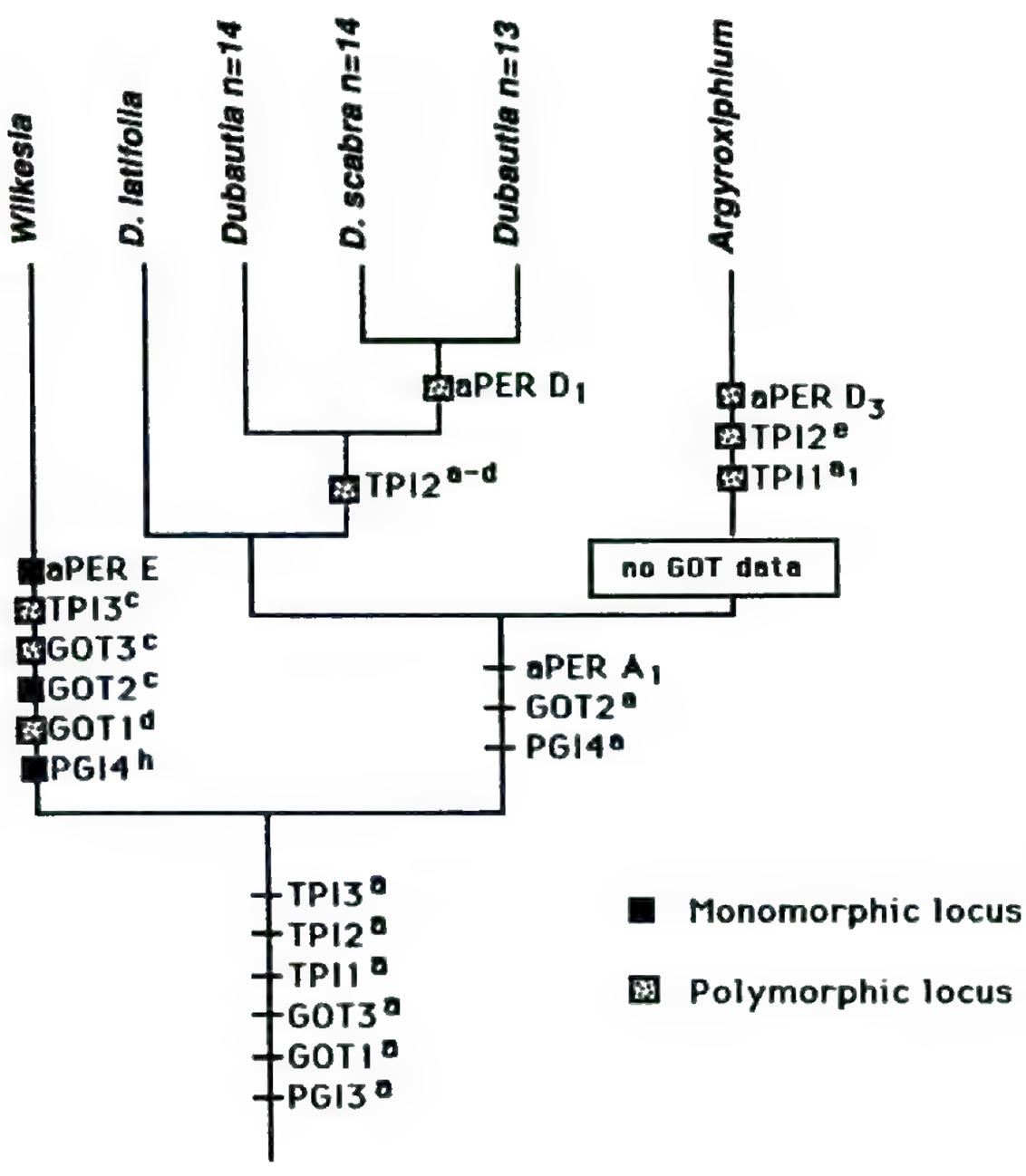

FIGURE 8. Distribution of unique alleles among the genera of the Hawaiian Madiinae. The tree format is used only to illustrate the distribution of alleles and does not represent actual phylogenetic relationships.

species of *Wilkesia* (Fig. 3) is significant to understanding the diversity within the Hawaiian Madiinae. Biogeographically and genetically (Fig. 5) the genus *Wilkesia* appears to be relatively ancient within Hawaii. However, speciation within the genus itself has been a much more recent phenomenon, and evolution even on the oldest major Hawaiian island, where *Wilkesia* is endemic, has not been static. The modern diversity of the Hawaiian Madiinae exists not only as the result of the accumulated products of ancient evolutionary events, but also because even the most ancient groups have continued to diversify and speciate.

In considering the distribution of unique alleles among the species of Hawaiian Madiinae, the shared alleles are generally taken to indicate common ancestry. However, accurately reconstructing phylogenetic relationships by the distribution of unique alleles is confounded by the fact that alleles originate in a polymorphic state and may persist for long periods as polymorphisms. Under these conditions the random loss of a synapomorphic allele may be fairly frequent, and true members of a clade may be excluded due to loss of alleles. Figure 5 illustrates just one of the possible tree topologies that can be generated using unique alleles with the

MacClade program (Maddison & Maddison, 1987). It shows that a single isozyme character is consistent with the cytological, morphological, and distributional data supporting *D. scabra* as the 14-paired species most closely related to the 13-paired taxa of *Dubautia*. Several species pairs that morphologically appear to be closely related are supported by the enzyme data: *D. reticulata* and *D. dolosa*; *D. sheriffiana* and *D. herbstobatae*; *D. paleata* and *D. raillardioides*; *D. pauciflorula* and *D. knudsenii* (Fig. 5).

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NEW *THELYPTERIS* (THELYPTERIDACEAE) FROM CENTRAL AMERICA

Alan R. Smith[1]

ABSTRACT

Studies on *Thelypteris* (Thelypteridaceae) for *Flora Mesoamericana* have revealed the following eight new species, which are herein described: *Thelypteris aureola*, *T. barvae*, *T. chiriquiana*, *T. croatii*, *T. grayumii*, *T. longisora*, *T. redunca*, and *T. subscandens*.

Thelypteris (subg. Goniopteris) **aureola** A. R. Smith, sp. nov. TYPE: Honduras. Yoro: Río Pelo, Cordillera de Mico Quemado, 60–380 m, 19 Mar. 1923, *Ames 136* (holotype, US). Figure 1D–E.

Ex affinitate *T. praetermissae* (Maxon) A. R. Smith, *T. nicaraguensis* (Fourn.) C. Morton, et specierum affinium glandibus stipitatis aureis vel auriantiacis abaxialiter abundantibus in axibus laminis sorisque distinguenda.

Rhizome not known, probably creeping; fronds 65 cm; petiole 32 cm × 3 mm; lamina 32 cm, with a conform apical pinna; buds lacking; pinnae 11 pairs, to 15 × 2.5 cm, incised ca. ⅔ their width, proximal ones abruptly narrowed but still lobed at their base; segments 4–5 mm wide, contiguous, suboblique and subfalcate; veins ca. 15 pairs per segment, proximal 2 pairs from adjacent segments connivent at sinus; indument abaxially on rachis, costae, veins, and laminar tissue of abundant golden or orangish, short-stipitate glands 0.1 mm, also with acicular hairs to 1 mm and stellate or furcate hairs less than 0.1 mm on costae and rachis, adaxially the laminar tissue with scattered sessile or short-stipitate glands; sori subcostular, exindusiate; sporangia and receptacle with numerous short-stipitate golden or orangish glands.

Known only from the type.

The lamina color in *T. aureola* is lighter, yellower green than in closely related species. Pubescence on the costae abaxially, a mixture of short, simple and furcate hairs less than 0.1 mm and stout simple hairs greater than 0.5 mm, suggests affinity with *T. praetermissa* (Maxon) A. R. Smith. Other close relatives include *T. minor* (C. Chr.) A. R. Smith and *T. nicaraguensis* (Fourn.) C. Morton. However, all of these are eglandular (as are most other members of subg. *Goniopteris*), in stark contrast to the copiously stipitate-glandular lamina of *T. aureola*. A few other species of *Thelypteris* apparently have entirely glandular variants in an otherwise hairy species, e.g., in *T. (Meniscium) longifolia* (Desv.) R. Tryon, and it is possible that this transformation is under simple genetic control. Nevertheless, it is a very striking and unusual feature and instantly makes the species recognizable.

Thelypteris (subg. Amauropelta) **barvae** A. R. Smith, sp. nov. TYPE: Costa Rica. Heredia: along Río San Rafael, Atlantic slope of Volcán Barva, 10°13′N, 84°05′W, 12 Apr. 1986, *Grayum 7012* (holotype, UC; isotype, MO). Figure 2A–C.

Thelypteris jimenezii affinis, a qua imprimis differt pinnis reductis basi laminae paucioribus (ca. 4-jugatis), segmentis latioribus sinubus angustioribus, textura crassiore, lamina abaxialiter parce pilosa, soris suboblongis.

Rhizome erect; fronds ca. 60 cm; stipe 13 cm × 2–3 mm, at base with numerous, ovate, persistent, shiny scales, these glabrous or with adpressed hairs 0.2–0.3 mm on surface; lamina ca. 45 cm, proximally with 4 pairs of subabruptly reduced pinnae, lowermost ca. 1 cm; pinnae opposite or subopposite, ca. 17 pairs, to 8 × 1.8 cm, incised to ca. 1.5–2 mm from costa; aerophores lacking; segments 5 mm wide; veins 6–7 pairs per segment; indument abaxially on rachis, costae, and costules of adpressed hairs 0.2–0.3 mm, laminar tissue abaxially glabrous or with a very few similar adpressed hairs; sori oblong or elongate along distal third of veins, exindusiate.

Known only from the type, in primary forest in low, damp places.

Perhaps most closely related to *T. jimenezii* (Maxon & C. Chr.) C. Reed but differing by having broader segments with narrower sinuses, thicker

[1] University Herbarium, University of California, Berkeley, California 94720, U.S.A.

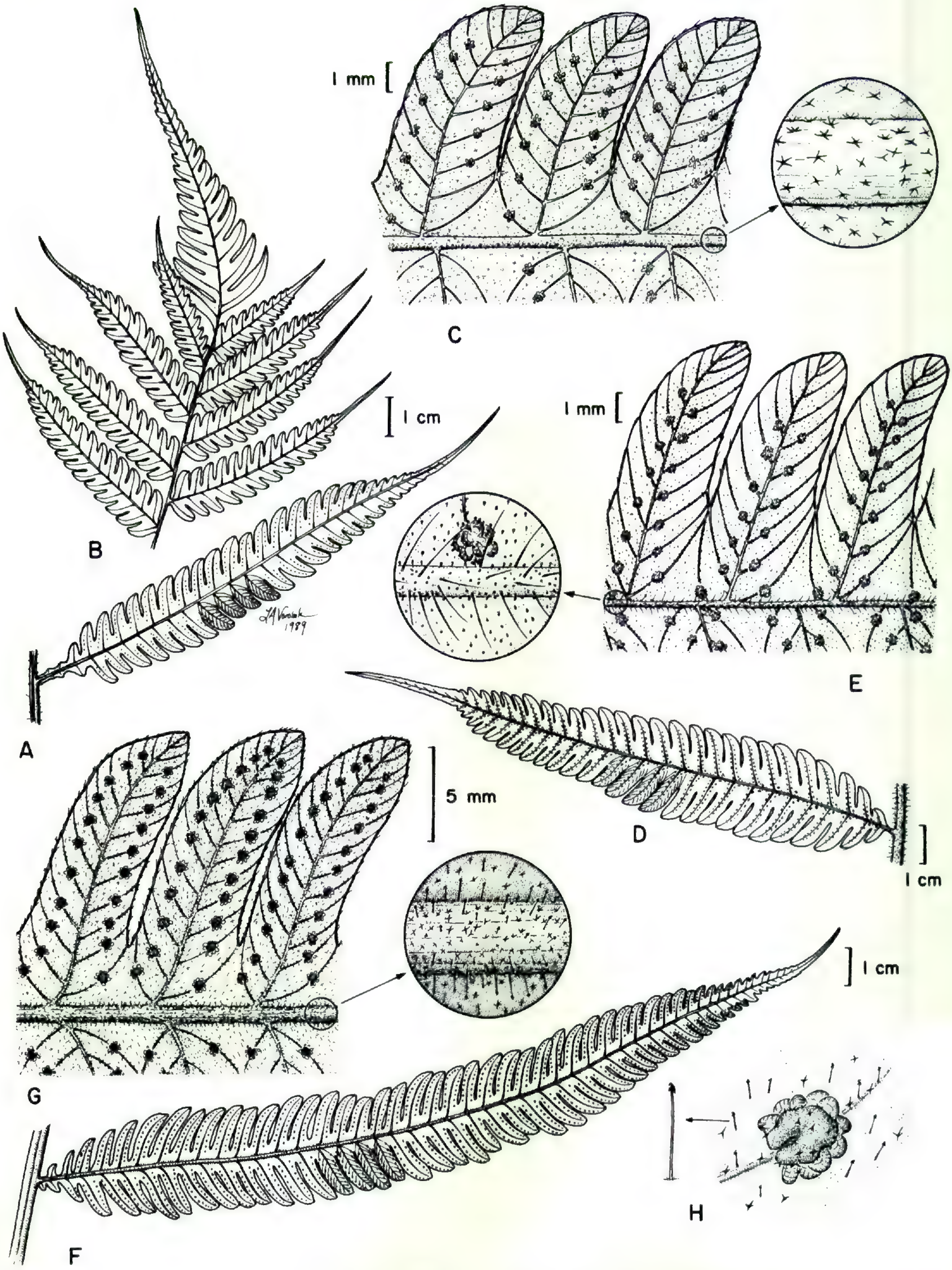

FIGURE 1. New species of *Thelypteris*. A–C. *Thelypteris croatii* (*Croat 21951* UC).—A.Proximal pinna.—B. Lamina apex.—C. Ultimate segments, with detail of hairs. D–E. *Thelypteris aureola* (*Ames 136* US).—D. Proximal pinna.—E. Ultimate segments, with detail of hairs and laminar glands. F–H. *Thelypteris redunca* (*Croat & Hannon 64239* UC).—F. Proximal pinna.—G. Ultimate segments, with detail of hairs.—H. Sorus.

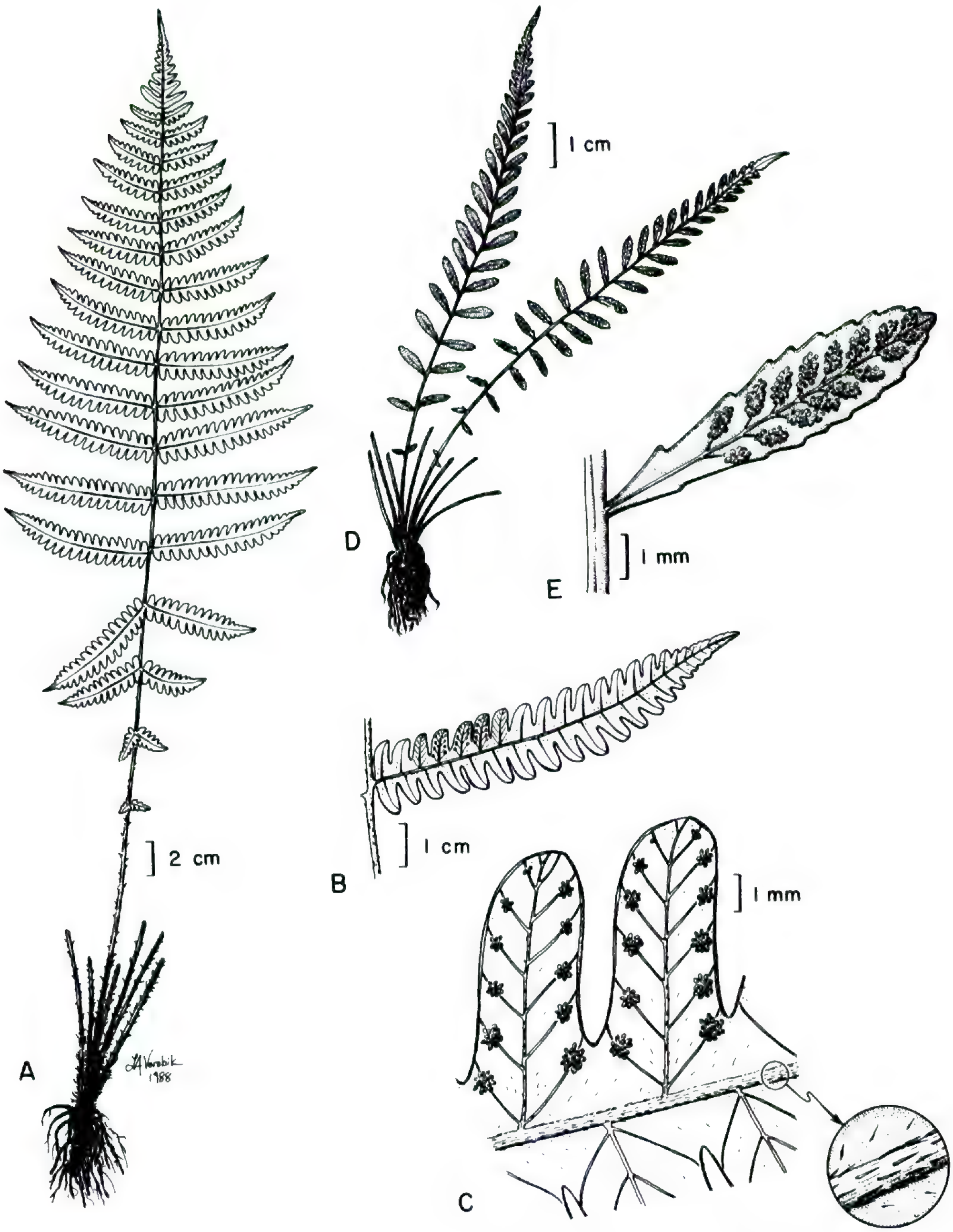

FIGURE 2. New species of *Thelypteris*. A–C. *Thelypteris barvae* (*Grayum 7012* UC).—A. Habit—B. Medial pinna.—C. Ultimate segments, with detail of hairs. D–E. *Thelypteris grayumii* (*Haber ex Bello & Lierheimer 4532* MO). —D. Habit.—E. Medial pinna.

lamina, laminar tissue glabrous abaxially and only sparingly hairy adaxially, elongate sori, and fewer reduced pinna pairs. In blade cutting, it greatly resembles certain species of sect. *Uncinella*, e.g., *T. atrovirens*, but hamate hairs are entirely lacking.

Thelypteris (subg. Amauropelta) **chiriquiana** A. R. Smith, sp. nov. TYPE: Panama. Chiriquí: Distrito Bugaba, Cerro Punta, from STRI house to edge of mountain across river, 8°52′N, 82°33′E, 2,200 m, 24 Jan. 1985, *van der Werff & Herrera 6319* (holotype, UC; isotype, MO not seen). Figure 3A–C.

Species indusiis amplis persistentibus fuscatis, pinnis subinaequilateris, stipitibus nitentibus, atropurpureis vel nigrescentibus, lamina eglandulosa et sparsim pilosa, rhizomate longo erecto gracili a congeneribus diversa.

Rhizome erect, caudex to 10 × 1 cm; fronds to 80 cm; petiole to ca. 15 cm × 2 mm, purple-

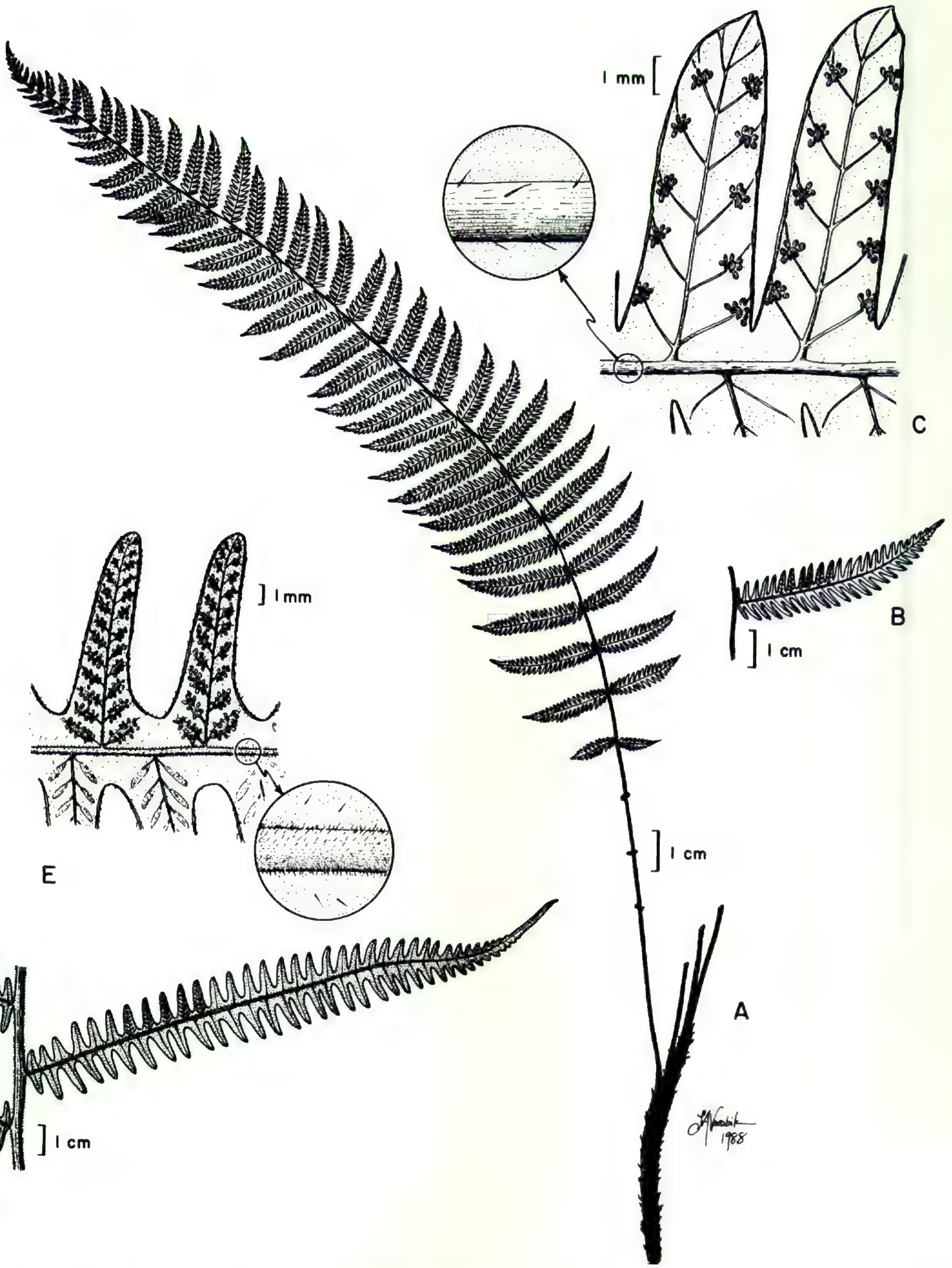

FIGURE 3. New Species of *Thelypteris*. A–C. *Thelypteris chiriquiana* (*van der Werff & Herrera 6319* UC).—A. Habit.—B. Medial pinna.—C. Ultimate segments, with detail of hairs. D–E. *Thelypteris longisora* (*van der Werff & Herrera 6375* UC).—D. Proximal pinna.—E. Ultimate segments, with detail of hairs.

black, shining, glabrous or with sparse hairs 0.1–0.2 mm, at base with castaneous, shining, glabrous scales to 5 × 1.5 mm; lamina to ca. 70 cm, proximally with ca. 6 pairs of subabruptly reduced pinnae, lowermost vestigial; pinnae to 6 × 1.5 cm, slightly inequilateral with segments on basiscopic side shorter and more oblique; aerophores absent or very weakly developed; segments ca. 3 mm wide; veins to 6 pairs per segment; indument abaxially lacking or of sparse hairs 0.1–0.2 mm on costae,

laminar tissue glabrous on both sides or sparsely short-hairy adaxially; sori medial to supramedial; indusium tan to dark brown, persistent, glabrous.

Known only from the type, from cloud forest.

Affinities of this species are uncertain. In the relatively large, darkened indusium and slightly inequilateral pinnae, it resembles *T. cinerea* (Sodiro) A. R. Smith but differs by having shining, purplish black stipe, eglandular lamina, and long, slender, erect rhizome.

The specimen *van der Werff & Herrera 6455* (UC), from the same area as the type, is similar but differs in the more numerous hairs on rachis and costae abaxially; scattered castaneous, linear scales to 0.5 mm on costae abaxially; tuberculiform aerophores; ciliolulate indusia; and creeping to ultimately suberect rhizome. These differences may be sufficient to recognize it as a different species, but more material is needed. The two are more closely related to each other than to other *Thelypteris*.

Thelypteris (subg. Goniopteris) **croatii** A. R. Smith, sp. nov. TYPE: Panama. Chiriquí: Burica Peninsula, Rabo de Puerco, 8 km W of Puerto Armuelles, 50–150 m, 18 Feb. 1973, *Croat 21951* (holotype, UC; isotype, MO). Figure 1A–C.

Ex affinitate *T. biolleyi* (Christ) Proctor et specierum affinium pilis ancyriformibus carentibus, venis infimis ad sinum conniventibus, basi pinnarum infimarum peranguste cuneata distincta; a *T. nephrodioides* (Klotzsch) Proctor soris exindusiatis vel indusiis minutis dignoscenda.

Rhizome erect; fronds ca. 1 m; stipe ca. 45–60 cm; lamina 50 cm, with a confluent, pinnatifid apex; buds lacking; pinnae ca. 20–25 pairs, to ca. 15 × 2.5 cm, incised ca. ¾–⅘ their width, proximal ones abruptly narrowed toward their long-cuneate base; segments ca. 4–6 mm wide; veins ca. 10–13 pairs per segment, proximal pair from adjacent segments connivent at sinus, rarely united below sinus; indument abaxially on rachis, costae, and veins entirely of sessile stellate hairs 0.1 mm, laminar tissue verrucose, with appressed stellate hairs on both sides, adaxially the veins with curved acicular hairs on costules; sori exindusiate or with an indusial fragment; sporangia with sessile stellate and simple hairs.

Paratypes. COSTA RICA. PUNTARENAS: between Las Cruces Botanical Garden and Río Jaba, ca. 3 km SE of San Vito de Coto Brus, 8°47′N, 82°58′W, 1,050–1,200 m, *Grayum 5606* (MO); San José: 13 km SW of San Isidro on road to Dominical, 800 m, 10 Aug. 1967, *Lellinger 878* (MO, US not seen). PANAMA. CHIRIQUÍ: along road from Puerto Armuelles to San Bartolo Limite, 7 mi. W of Puerto Armuelles, ca. 120 m, 19 May 1976, *Croat 35064* (MO).

This belongs to the group of *T. biolleyi* (Christ) Proctor but differs in the complete absence of anchor-shaped hairs and in the lowermost pair of veins connivent at the sinus, occasionally united below the sinus. From *T. nephrodioides* (Klotzsch) Proctor, *T. croatii* differs in being exindusiate or with only a minute fragmentary indusium. From both it differs in the narrowly cuneate pinna bases.

Thelypteris (subg. Amauropelta) **grayumii** A. R. Smith, sp. nov. TYPE: Costa Rica. Heredia: along Río San Rafael, Atlantic slope of Volcán Barva, 10°13′N, 84°05′W, 1,500 m, 12 Apr. 1986, *Grayum 7042* (holotype, UC; isotype, MO not seen). Figure 2D–E.

Thelypteris villanae affinis, a qua imprimis differt pinnis infimis 1–2 paribus pinnarum aliquantum reductarum, 3–5 mm longis (non valde reductis), basi stipitum exsquamatis, pinnis integris vel crenulatis, ascendentibus, basin versus cuneatis.

Rhizome suberect; fronds 5–15 cm, fasciculate; stipe up to 2 cm × 0.7 mm, tan to brownish, glabrous; lamina to ca. 13 cm, proximally with 1 or 2 pairs of slightly shortened pinnae, lowermost ca. 3–5 mm long, distally the lamina pinnatifid and somewhat attenuate; pinnae alternate, often strongly ascending, up to ca. 15 pairs, up to 10 × 2.5 mm, narrowed at the base, entire to crenulate, sometimes with a single acroscopic, nearly free basal lobe; aerophores lacking; veins simple from the costae, up to ca. 10 pairs per pinna; indument completely lacking on both sides of lamina; sori oblong or elongate along the proximal ½–⅔ of the veins, exindusiate.

Paratype. COSTA RICA. PUNTARENAS: Monteverde Cloud Forest Reserve, road to TV towers, 10°20′N, 84°50′W, 1,600 m, 23 Apr. 1986, *Haber ex Bello & Lierheimer 4542* (MO).

This is probably most closely related to *T. villana* L. D. Gómez, from which it differs in fronds lacking strongly reduced proximal pinnae (2–4 pairs reduced in *T. villana*, the lowest ca. 1 mm long), in the completely glabrous stipe (scaly stipe bases in *T. villana*) in the more ascending pinnae that are narrowed at the base, and in growing at higher elevations (200–1,100 m for *T. villana*). The holotype was noted as growing on mossy boulders in a river.

The species is named for its collector, Dr. Michael Grayum, who brought it to my attention as possibly new, and who has made many important collections of and observations on Costa Rican pteridophytes.

Thelypteris (subg. Amauropelta) **longisora** A. R. Smith, sp. nov. TYPE: Panama. Chiriquí: Distrito Bugaba, Cerro Punta, from STRI house to nearby ridge, 2,200 m, 8°52′N, 82°33′W, 25 Jan. 1984, *van der Werff & Herrera 6375* (holotype, UC; isotype, MO not seen). Figure 3D–E.

Species soris elongatis secus venas, frondibus ad 2 m longis, pinnis profunde incisis, sinubus inter segmenta latis, pilis hamatis carentibus, abaxialiter squamis appressis amorphis secus costas a congeneribus diversa.

Rhizome erect; fronds to 2 m; stipe length unknown, 5+ mm diam.; lamina to ca. 1.5 m, proximally with 5+ pairs of abruptly reduced pinnae, lowermost vestigial; pinnae 30 pairs or more, to 20 × 3 cm, incised within 1 mm of costa; aerophores lacking or tuberculiform; segments to 5 mm wide, sinuses very broad; veins to 20 pairs per segment; indument abaxially of dense, short hairs 0.1 mm long on rachis, costae, and costules, also with a few appressed amorphous costal scales (irregular in shape and lacking obvious cell definition) to 1 mm, lamina adaxially with spreading slightly reddish hairs 0.2–0.3 mm; sori linear, running along half to nearly the entire length of veins, confluent and completely obscuring the lamina at maturity; exindusiate.

Known with certainty only from the type, from cloud forest.

In the flora area, only *T. linkiana* (C. Presl) R. Tryon and *T. atrovirens* (C. Chr.) C. Reed have the sori so elongate along the veins, but these species both bear hamate hairs on the axes abaxially. Other characters distinguishing *T. longisora* are the very broad sinuses between segments, deeply incised pinnae, fronds to 2 m with widely spaced pinnae, and appressed, amorphous scales on the costae abaxially.

The specimen *Smith et al. 2446* (UC), from the same general area as the type, is nearly identical in lamina dissection and sorus shape but differs in the costae and rachis abaxially lacking hairs and having more numerous costal scales.

Thelypteris (subg. Goniopteris) **redunca** A. R. Smith, sp. nov. TYPE: Honduras. Olancho: along Río Olancho, on road between San Francisco de la Paz and Gualaco, 13.6 mi. SW of Gualaco, 15°00′N, 86°07′W, 1,300 m, 6 Feb. 1987, *Croat & Hannon 64239* (holotype, UC; isotype, MO not seen). Figure 1F–H.

Thelypteris biolleyi affinis, a qua imprimis differt venis infimis ad sinum margine attingentibus, pinnis profunde incisis, indusiis magnis persistentibus rufo-brunneis, pilis abaxialiter ancyriformibus et densioribus ad laminam venasque.

Rhizome apparently short-creeping; fronds ca. 140 cm; petiole ca. 70 cm × 5 mm; lamina ca. 70 cm, gradually narrowed distally to a confluent, pinnatifid apex; buds lacking; pinnae ca. 20 pairs, to 22 × 3 cm, deeply incised to within 2 mm of costa, basal segments of proximal pinnae free or nearly so, reduced; segments 4–5 mm wide, acutish at apex, subfalcate; veins to ca. 15 pairs per segment, proximal pair from adjacent segments meeting margin at or just above sinus; indument abaxially of dense anchor-shaped hairs 0.2–0.3 mm and stellate hairs on costae, veins, and laminar tissue, adaxially with appressed stellate hairs; sori with a large, reddish brown indusium, this stellate-hairy; sporangia glabrous.

Known only from the type.

This is most closely related to *T. biolleyi* (Christ) Proctor but differs in having the lowermost pair of veins meeting the margin at the sinus; deeply incised pinnae; large, persistent, reddish brown indusia; and denser covering of anchor-shaped hairs on the lamina and veins abaxially. Another close relative, *T. nephrodioides* (Klotzsch) Proctor, differs in lacking anchor-shaped hairs and in being less deeply incised. *Thelypteris croatii* differs in lacking anchor-shaped hairs and in being nearly or quite exindusiate.

Thelypteris (subg. Amauropelta) **subscandens** A. R. Smith, sp. nov. TYPE: Costa Rica. Heredia: N end of Cerros Las Marías, N slope of Volcán Barva, 10°10.5′N, 84°06.5′W, 2,100–2,380 m, 19 Apr. 1986, *Grayum 7273* (holotype, UC; isotype, MO not seen). Figure 4.

Species rhizomate scandenti, ad 1 m × 4 mm, rhachidi costis costulisque abaxialiter pilis hamatis 0.2–0.3 mm praeditis, lamina adaxialiter pilis adpressis carenti, costis abaxialiter squamis parvis castaneis praeditis, indusiis persistentibus, 0.7–1.0 mm, atrocastaneis vel nigrescentibus epilosis a congeneribus diversa.

Rhizome prostrate to subscandent (erect on smaller plants), to 1 m × 4 mm, bearing ovate to ovate-lanceolate, castaneous, glabrous, shining scales 2–3 × 1–1.5 mm; fronds ca. 75 cm; stipe to ca. 15 cm × 2–3 mm, dark brown at base, with numerous hairs 0.1–0.3 mm, these slightly reddish, often ± appressed; lamina to ca. 60 cm, proximally with ca. 4 pairs of abruptly reduced pinnae, lowermost ca. 1 mm; pinnae alternate, ca. 30 pairs, to 10 × 2.2 cm, deeply incised to within 0.5 mm of costa; aerophores lacking; segments ca. 3 mm wide, suboblique, margin entire to crenulate; veins to ca. 10 pairs per segment; indument abaxially on rachis, costae, and costules of spreading, hamate hairs 0.2–0.3 mm, laminar tissue glabrous

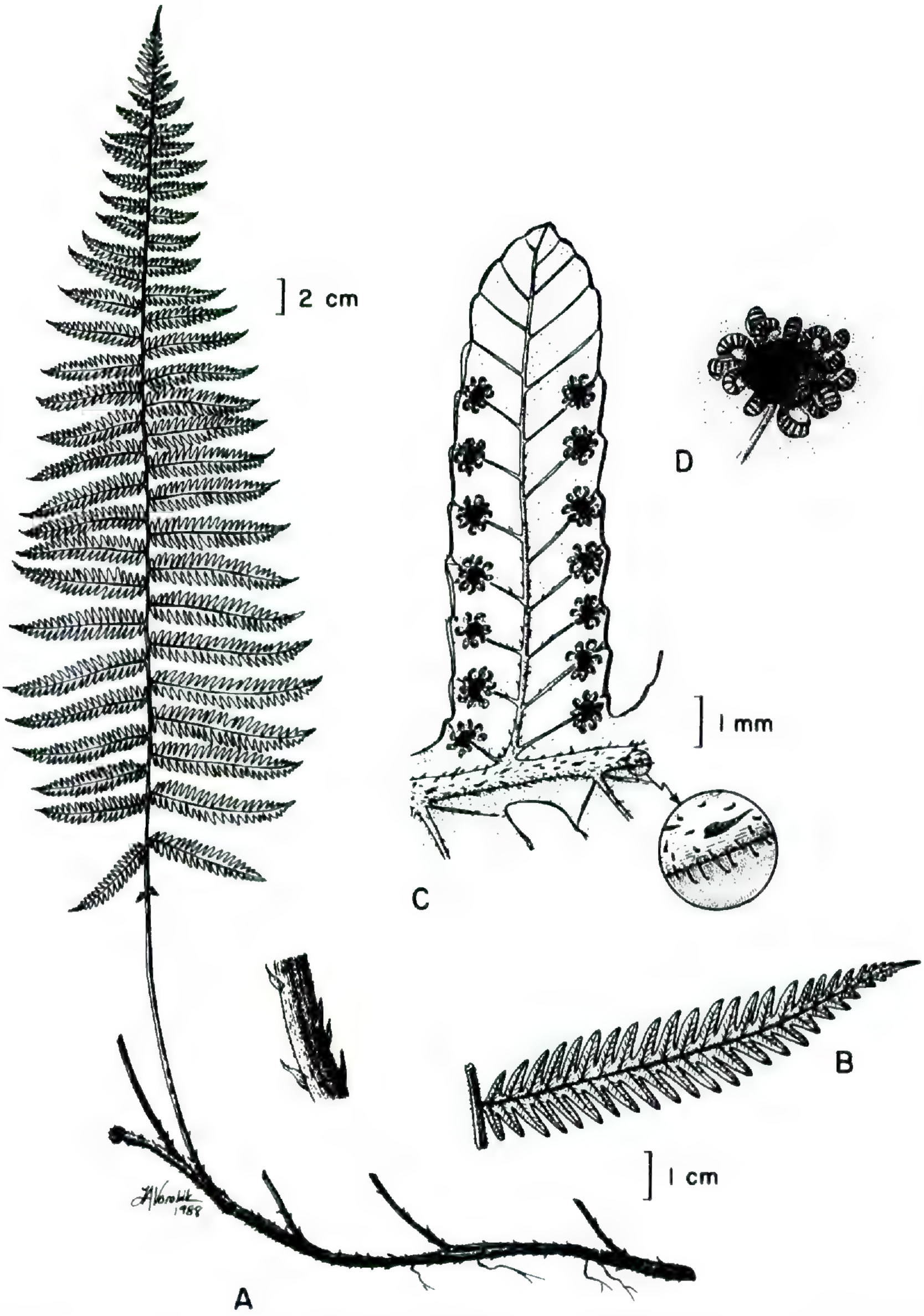

FIGURE 4. *Thelypteris subscandens* (*Grayum 7273* UC).—A. Habit.—B. Medial pinna.—C. Ultimate segments, with detail of hairs.—D. Sorus.

or nearly so on both sides; sori round, supramedial, with a relatively large, persistent indusium ca. 0.7–1.0 mm diam., this dark-castaneous to blackish with a very narrow tan margin, minutely glandular at the margin, epilose.

Known only from the type, from cloud forest on ridge.

The hamate hairs suggest that this species belongs to sect. *Uncinella*. However, *T. subscandens* differs remarkably from all known members of the section by the scandent rhizome. Also, it lacks adpressed hairs on the lamina adaxially, a character found in most other members of the section. In addition, it bears small castaneous scales on the costae abaxially. In sum, it is one of the more distinctive species in the section, perhaps in all of the subgenus, and close relatives are not apparent.

THE GRASSES OF CHIQUITANIA, SANTA CRUZ, BOLIVIA[1]

Timothy J. Killeen[2]

Abstract

A checklist is provided for the Gramineae of the Brazilian Shield region in eastern Santa Cruz, Bolivia. Annotations include keys to genera and species, a regional synonymy, notes on habitat preference, geographic distribution, cytology, phenology, and palatability for 275 species of tropical grasses; six new taxa are described: *Andropogon sanlorenzanus*, *Eragrostis chiquitaniensis*, *Eriochrysis* ×*concepcionensis*, *Paspalum kempffii*, *Schizachyrium beckii*, and *Thrasya crucensis*.

Chiquitanía is a region in eastern lowland Bolivia which includes the Provinces of Ñuflo de Chávez, Velasco, and Chiquitos in the Department of Santa Cruz. Recognized as a distinct cultural and geographic region, it has a unique natural history when compared with other parts of eastern Bolivia. Situated on the extreme western edge of the Brazilian (Precambrian) Shield, it is characterized by a variable topography (altitude 300–1,240 m) that supports a high diversity of forest, savanna, and savanna wetland communities. Encompassing approximately 170,000 km², Chiquitanía is bordered on the south by the Serranías Chiquitanas, to the west by the alluvial plains of central Santa Cruz, to the east by the Gran Pantanal of Brazil, and to the north by the Department of the Beni (Fig. 1). Although it was colonized over 250 years ago by Jesuit missionaries, the vegetation of the region remains largely unaltered as the local inhabitants have utilized the native savanna for cattle production while exploiting the forest for timber, rubber, or wildlife. Shifting agriculture, while common, does not currently pose a threat to the existing forest vegetation. However, the recent introduction of exotic forage grasses adapted to forest soils threatens to disrupt traditional patterns of agriculture. Due to increased productivity and better nutritional quality, these grasses allow for higher stocking rates and the easier management of cattle. Consequently, forest destruction for pasture establishment is occurring at accelerated levels. It is hoped that a better understanding of the native grasses will promote range management techniques which improve the productivity of savanna vegetation, while at the same time helping to preserve some natural communities. This checklist is the partial result of three years of work in the region studying the autecology of the native grasses. Analytic results of the autecological investigations, as well as general descriptions of the vegetation, will be reported in future publications.

Climate

The region has a typical savanna climate or "Aw" in the Koppen classification. The regional airport at Concepción (16°03′S, 62°10′W; altitude 500 m), has meteorological data spanning 35 years (Guamán & Valverde, 1982). Mean annual precipitation is about 1,200 mm with a marked dry season of five months during the austral winter. Annual fluctuations vary greatly, ranging from 700 mm to 1,500 mm. Mean daily temperature varies only slightly throughout the year, reaching a maximum in November (26°C) and a minimum in June (21°C). Strong cold fronts sweep through the region during the dry season, causing the temperature to drop to 10°C for short periods. Maximum temperatures of about 33°C are common in November at the beginning of the rainy season.

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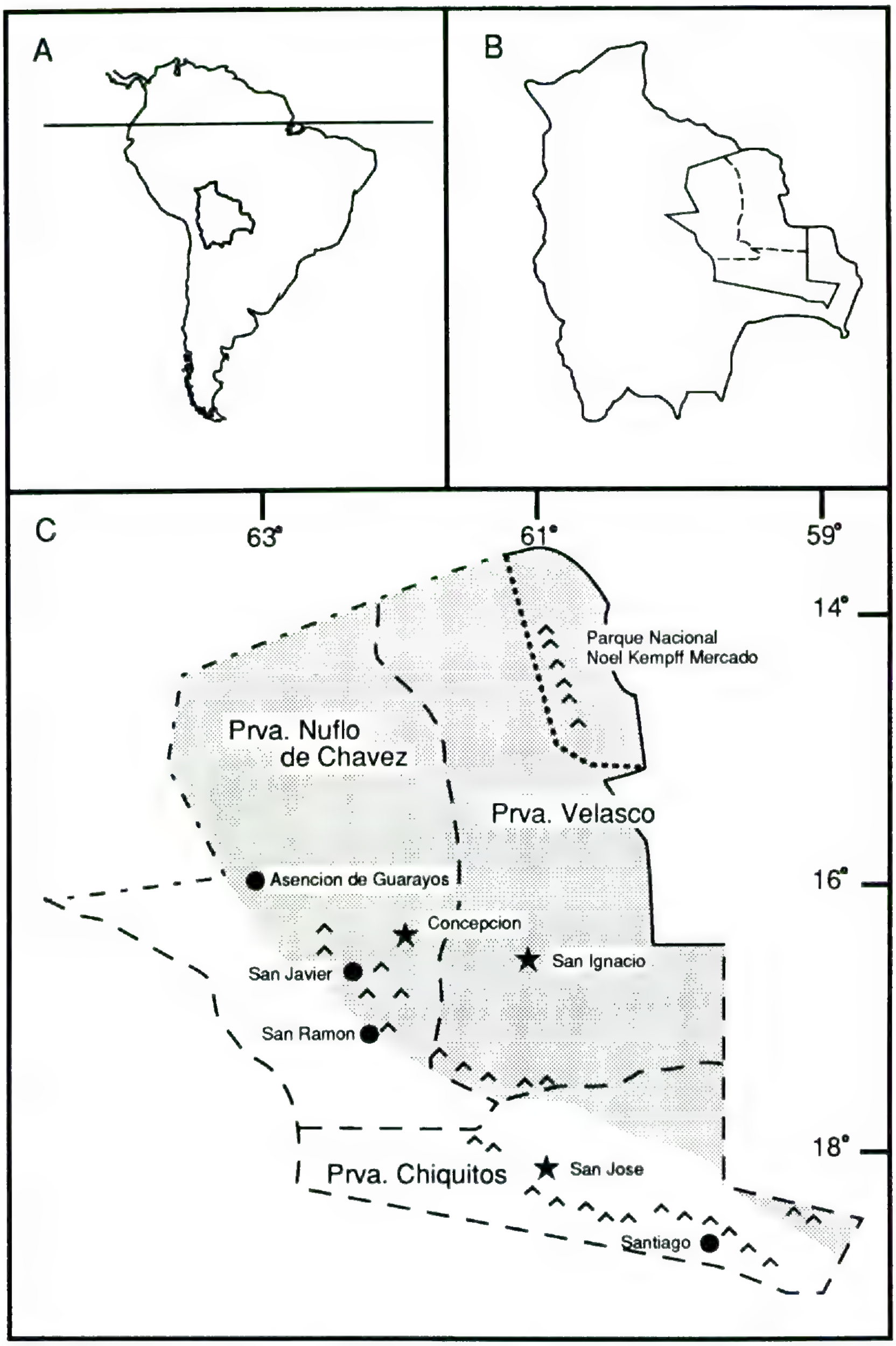

FIGURE 1.—A. Map of South America showing Bolivia. -B. Geographic position of Chiquitanía within Bolivia.—C. Chiquitanía in detail: stippled area corresponds to the Brazilian (Precambrian) Shield; stars represent provincial capitals; dots are other large villages; and carats mark serranías or hill country. A solid line marks the international border with Brazil, a dash/dot line demarcates the Department of Santa Cruz from the Beni, dashed lines mark provincial boundaries, and a dotted line delimits the boundary of Parque Nacional "Noel Kempff Mercado."

VEGETATION

The vegetation in Chiquitanía is similar to that described for the adjacent regions of central Brazil and, although Bolivians have developed their own vernacular terms for describing the vegetation in Chiquitanía, I use the standard terminology developed by Brazilian ecologists (Eiten, 1972, 1978; Ratter et al., 1988). *Cerrado* refers to a complex of intergrading communities that range from low forest to open grassland and that are characterized by the presence of tortuous, woody species with thick stems and coriaceous leaves. *Cerrado* is the most common savanna vegetation in Chiquitanía and is usually restricted to eroded Tertiary planation surfaces or the upper slopes of low hills (500–700 m). Easily recognized due to its distinctive physiognomy, these well-drained savanna communities are western disjuncts separated from the *cerrado* province of central Brazil by the more

TABLE 1. A comparison of the floristic similarity of the grasses of Chiquitanía with other neotropical floras.

Geographic region	Source	Total species[1]	Species in common	Index of similarity[2]
Chiquitanía	This study	250	—	—
Andean Piedmont of Santa Cruz, Bolivia	Foster (1966) and others[3]	120	100	53
Llanos de Mojos, Beni and northeastern La Paz, Bolivia	Beck (1984) Haase & Beck (1989)	112	78	43
Paraná, Brazil	Renvoize (1988)	329	120	40
Bahia, Brazil	Renvoize (1984)	331	114	39
Santa Catarina, Brazil	Smith et al. (1982)	343	108	36
Costa Rica	Pohl (1980)	392	108	33
Entre Ríos, Argentina	Burkhart (1969)	319	79	28
Central Andes	Hitchcock (1927)[4]	642	123	27
Tucumán, Argentina	Türpe (1975)	298	57	21

[1] Excludes cultivated grasses and those species included by the authors that occur only in adjacent regions.
[2] Sørensen (1948):

$$\text{index} = \frac{\#\text{ of species in common to A \& B}}{(\#\text{ of species in A} + \#\text{ of species in B})(0.5)} \times 100.$$

[3] Consisting mainly of the collections of José Steinbach as cited by Foster (1966) and additional collections known to the author, particularly those of Michael Nee (NY).
[4] Excludes species recorded only from the Andean Piedmont of Santa Cruz (i.e., the collections of José Steinbach).

abundant, seasonal forest vegetation. The Bolivians refer to this vegetation as *pampa arbolada* or *arbolada*. Floristically and structurally distinct from *cerrado* is a xerophytic savanna complex known as *campo rupestre* (Eiten, 1978). This treeless savanna occurs as islands restricted to ridge tops 800–1,200 m above sea level. There are a number of *campo rupestre* localities in eastern Santa Cruz, of which the western escarpment of the Serranía de Caparuch (i.e., Parque Nacional "Noel Kempff Mercado") is probably the most extensive. The Serranía de San Lorenzo, situated near the town of San Javier, is only 40 km from the western edge of the Brazilian Shield (16°15′S, 62°40′W; altitude 900 m) and is one of the most western *campo rupestre* localities in South America. This site has yielded two new grass species and several unique intraspecific variants; undoubtedly, more taxa will be described as the flora of this serranía is documented. The locals refer to this vegetation type as *campo* or *pampa*, distinguishing it from *cerrado* (*pampa arbolada*) by the lack of woody vegetation.

Similarly, the wetland communities common to central Brazil occur throughout Chiquitanía. *Valley-side campos* are treeless savannas that occur along erosional surfaces, wherever there is a fluctuating, perched, water table that seeps out on gently sloping valley sides (Eiten, 1978; Goldsmith, 1974). The overflow of rivers on alluvial plains leads to the formation of a *pantanal* complex of *seasonally humid* or *seasonally inundated savannas* (Cole, 1986; Eiten, 1978). Scattered across these open grasslands are raised earth platforms built up by termites; these support *cerrado* species or low forest. At the base of valley-side *campos* and scattered across the *pantanal* complexes one finds *savanna marsh*, a savanna wetland community with saturated soils throughout the year. Beck (1984) and Haase & Beck (1989) reported on similar extensive savanna wetlands in the Department of Beni. The residents of Chiquitanía generally refer to all savanna wetlands as *curiches*.

Ruiz (1982) conducted a preliminary inventory of the *seasonal forest* communities near Concepción in the Province of Ñuflo de Chávez. The forest

TABLE 2. The geographic distribution of the grasses recorded to occur in Chiquitanía, Santa Cruz, Bolivia.

Pantropical	Neotropical	South American	Southern Cone[1]	Central Brazil[2]	Central Andes	Bolivian endemics	Other[3]
33	103	38	27	38	2	7	25

[1] Includes central and southern (extra-amazonian) Brazil, Bolivia, Paraguay, Uruguay, and subtropical regions of Argentina.
[2] Includes central Brazil and adjacent *cerrado* regions in Bolivia and Paraguay.
[3] Cultivated grasses and species only collected in adjacent regions of Bolivia.

TABLE 3. Synopsis of the tribes and genera (number of species occurring in Chiquitanía).

Bambuseae (8)
Actinocladum, Bambusa, Chusquea, Guadua, Rhipidocladum

Olyreae (4)
Olyra

Streptochaeteae (1)
Streptochaeta

Phareae (1)
Pharus

Oryzeae (7)
Leersia, Luziola, Oryza

Centotheceae (1)
Orthoclada

Arundineae (2)
Arundo, Gynerium

Aristideae (13)
Aristida

Pappophoreae (2)
Pappophorum

Eragrostideae (24)
Dactyloctenium, Eleusine, Eragrostis, Gouinia, Leptochloa, Tripogon

Cynodonteae (9)
Chloris, Cynodon, Eustachys, Gymnopogon, Microchloa

Sporoboleae (6)
Sporobolus

Paniceae (144)
Acroceras, Anthaenantiopsis, Arthropogon, Axonopus, Brachiaria, Cenchrus, Digitaria, Echinolaena, Echinochloa, Eriochloa, Homolepis, Hymenachne, Ichnanthus, Lasiacis, Leptocorypheum, Melinis, Mesosetum, Oplismenus, Otachyrium, Panicum, Paspalum, Pennisetum, Rhynchelytrum, Sacciolepis, Setaria, Thrasya

Arundinelleae (3)
Arundinella, Loudetia, Loudetiopsis

Andropogoneae (51)
Agenium, Andropogon, Bothriochloa, Coelorhachis, Elionurus, Eriochrysis, Hackelochloa, Hemarthria, Hyparrhenia, Imperata, Rhytachne, Saccharum, Schizachyrium, Sorghastrum, Sorghum, Trachypogon, Tripsacum, Zea

types described in his study are semideciduous, and the density of the understory is inversely correlated with the development of the canopy. High forest was described as having canopy trees 20–25 m tall and formed one end of a continuum of forest or forest scrub communities that eventually intergrade with *cerrado*. In contrast, *gallery forest*, which occurs as a narrow strip 50 to 100 m wide on valley floors, is an evergreen community with trees 15–30 m tall. Locally, the various gradations of forest are recognized and referred to as *monte alto, monte bajo*, and *monte humedo*. In addition, *granitic outcrops*, locally known as *lajas*, exist as islands within *cerrado, campo rupestre*, savanna wetlands, and seasonal forest. These range in size from small outcrops scattered across the landscape to large domes (inselbergs) that can attain a height of 200 m and diameter of 400 m or more.

FLORISTIC RELATIONSHIPS OF THE GRASSES OF CHIQUITANÍA

This is the first relatively complete inventory of native grasses from a region in central South America. Table 1 compares the number of species shared with grass floras of Costa Rica, Brazil, Argentina, the Central Andes, and two adjacent regions in eastern Bolivia. The greatest similarity is with the grass flora of the Bolivian savanna regions, followed by the floras of the coastal states of Brazil. Chiquitanía shows little floristic affinity with the high altitude grasslands of the Andes or with the subtropical grasslands of Argentina. The similarity to the Brazilian floras is even more apparent when the species are classified according to their geographic distributions (Table 2).

The Bolivian plant collector José Steinbach made extensive collections of grasses near the town of Buenavista on the Andean Piedmont in western Santa Cruz (Foster, 1966). If one assumes that his collections are an essentially complete inventory of the grasses for that region, then the richness of the grass flora of the Brazilian Shield becomes apparent. One hundred thirty more species have been recorded for Chiquitanía than for the Andean Piedmont even though the two areas have a high index of similarity. Only 20 species collected on the Andean Piedmont have not also been recorded for Chiquitanía. The greater species richness of Chiquitanía is most easily explained by the greater diversity of savanna communities in the region, and in part possibly by richness within the savannas. A similar argument can be made to explain the greater number of species reported for the extensive savanna wetlands of the Beni; however, this remote part of Bolivia has yet to be inventoried adequately. This study documents 80 new records for Bolivia, including two genera *Actinocladum* and *Streptochaeta*, and 112 new records for the Department of Santa Cruz. A total of 75 genera and 276 species are reported here (Table 3).

In addition to the key, annotations for each

taxon include citations of recent monographic treatments, regional synonymies (Brazil, Argentina, Uruguay, Paraguay, and the Central Andes), discussion of selected taxonomic problems, notes on habitat preferences, geographic distributions (information collated from existing floras and monographs), palatability, local flowering behavior (peak months italicized), and cytology. Fire is crucial in initiating flowering for many species and these can be found in bloom between July and November at the end of the dry season when ranchers systematically burn native savannas to provide forage for cattle. Palatability estimates (0–4) are based on paired comparisons along fences dissecting overgrazed and lightly grazed savanna (unpublished data), as well as observations made of selective grazing by cattle. Species ranked as (0) either increased in relative abundance or showed no effect in response to overgrazing; a ranking of (1) is given to species that showed no evidence of grazing but were found to be less abundant in overgrazed savannas; rankings of (2–4) are for species that decrease in relative abundance in overgrazed savannas and/or were observed to be grazed selectively by cattle. Chromosome counts are based on meiotic squashes made in the field and are being independently verified via mitotic preparations (Norman, Quarin & Killeen, in prep.). Specimens cited are those of the author unless otherwise indicated; boldface numbers are voucher specimens for cytological preparations and usually have a matched set of seeds, which has been sent to the Instituto de Botánica del Nordeste in Corrientes, Argentina (CTES). The distribution of replicate sets of specimens are as follows: Iowa State University (ISC), Herbario Nacional de Bolivia (LPB), Field Museum of Natural History (F), Missouri Botanical Garden (MO), United States National Herbarium (US), New York Botanical Garden (NY), Instituto de Botanica Darwinión, San Isidro, Argentina (SI), and Instituto de Botanica del Noreste, Corrientes, Argentina (CTES).

Key to Genera

KEY TO GROUPS

1a. Giant grasses; woody or semiwoody; culms 2–30 m tall ..... Key I
1b. Not giant grasses; culms herbaceous or rarely semiwoody; plants prostrate or up to 2 m tall.
  2a. Leaf blades constricted at the base into pseudopetiole, the blades lanceolate or ovate; forest grasses .. Key II
  2b. Leaf blades lacking pseudopetiole, the blades linear, lanceolate, or ovate; plants of various habitats.
    3a. At least some spikelets disarticulating with attached bristles, involucres, rachis internodes, and pedicels, or (rarely) spikelets persistent on the inflorescence and not disarticulating ..... Key III
    3b. Spikelets disarticulating without any attached bristles, rachis internodes, or pedicels.
      4a. Spikelets disarticulating above the persistent glumes (glumes and lemmas falling in some species of *Eragrostis* but then the palea and rachilla persistent); spikelets 1–many-flowered ..... Key IV
      4b. Spikelets disarticulating below the glumes (glumes vestigial in some genera); spikelets 1–2-flowered ..... Key V

KEY I

Giant grasses; woody or semiwoody; culms 2–30 m tall.

1a. Foliage usually dimorphic: culms producing leaves with reduced, often deciduous blades, the branches with numerous overlapping leaves with well-developed, pseudopetiolate blades; plants blooming infrequently.
  2a. Nodes of culm with a dominant bud (or branch) and 1–many smaller branches, or with a single large branch having numerous secondary branches inserted at its basal nodes; branches thorny or not thorny.
    3a. Primary buds (or branches) at each midculm node solitary; secondary branches (if present) inserted at the basal nodes of the primary branch; plants arboreal; culms erect, stout, hollow, or solid at base and hollow towards apex; branches usually thorny, at least at the base of the plant ..... *Guadua*
    3b. Primary buds (or branches) at each midculm node numerous, with one large bud and numerous smaller buds (or branches), frequently the major bud remaining dormant and obscured by branches developed from the numerous minor buds; plants vining or scandent; culms solid; branches lacking thorns ..... *Chusquea ramosissima*
  2b. Nodes of culm producing several to numerous branches of equal size; branches not thorny.
    4a. Branches originating from a triangular shield above the node; forest liana ..... *Rhipidocladum racemiflorum*
    4b. Branches originating in a straight line; growing in open savanna or rarely in dense scrub ..... *Actinocladum verticillatum*
1b. Foliage not dimorphic, the leaves of culm and branches similar, lacking a pseudopetiole; plants blooming every year.
  5a. Spikelets bisexual.

6a. Inflorescence a spicate panicle; spikelets glabrous or pubescent but not villous, subtended by an involucre of bristles ..... *Pennisetum*
6b. Inflorescence a panicle or panicle of racemes; spikelets villous, not subtended by an involucre of bristles.
7a. Spikelets with 3–6 bisexual florets, the callus of the spikelet and glumes glabrous, the lemmas villous ..... *Arundo donax*
7b. Spikelets with 2 florets, the lower reduced to a single hyaline lemma, the callus villous, the glumes glabrous or pubescent, the lemmas glabrous to sparsely ciliate ..... *Saccharum*
5b. Spikelets unisexual.
8a. Plants dioecious; spikelets villous; inflorescence paniculate ..... *Gynerium sagittatum*
8b. Plants monoecious; spikelets not villous; inflorescence racemose or highly modified.
9a. Foliage basal and caulescent; staminate spikelets apical and pistillate spikelets basal on the same inflorescence; cultivated and wild plants ..... *Tripsacum*
9b. Foliage caulescent; staminate spikelets in terminal racemes and pistillate spikelets on axillary cobs; cultivated plants ..... *Zea mays*

KEY II

Grasses rarely approaching 2 m in height; culms herbaceous; leaf blades constricted at the base, forming a pseudopetiole, the blades lanceolate to ovate; forest grasses.

1a. Spikelets unisexual; plants monoecious.
2a. Pseudopetiole twisted, the abaxial side of the blade facing upward; staminate and pistillate spikelets paired with each other; lemma of pistillate spikelet coriaceous, with uncinate (hooked) hairs ..... *Pharus lappulaceus*
2b. Pseudopetiole not twisted, the adaxial surface of the blade facing upward; pistillate spikelets generally terminal on branches with staminate spikelets below; lemma of pistillate spikelet cartilaginous, glabrous or pubescent but lacking uncinate hairs ..... *Olyra*
1b. Spikelets bisexual.
3a. Pseudopetiole 3–40 mm long; blades with cross veins between the longitudinal veins clearly visible; spikelets terete or laterally compressed.
4a. Inflorescence a spike; spikelets terete, aristate, the awns becoming entwined when mature and causing the spikelets to fall as a group ..... *Streptochaeta spicata*
4b. Inflorescence a diffuse open panicle; spikelets laterally compressed, awnless ..... *Orthoclada laxa*
3b. Pseudopetiole shorter than 3 mm; blades lacking evident cross veins; spikelets dorsally compressed (glumes keeled in *Ichnanthus*).
5a. Spikelets subtended by sterile panicle branches; inflorescence a spicate panicle ..... *Setaria*
5b. Spikelets not subtended by sterile panicle branches; inflorescence not a spicate panicle.
6a. Both glumes equal ..... *Homolepis aturensis*
6b. Lower glume ½–⅔ the length of upper glume.
7a. Lemma of upper floret with a pair of winged appendages or scars at base ..... *Ichnanthus*
7b. Lemma of upper floret lacking winged appendages or scars at base.
8a. Spikelets subglobose, black at maturity, obliquely placed on pedicels; glumes and lower lemma with apical tufts of hairs ..... *Lasiacis*
8b. Spikelets elliptic or ovate, variously green or purple at maturity, not obliquely placed on pedicels; glumes and lower lemma variously glabrous to pubescent but apices lacking tufts of hairs ..... *Panicum*

KEY III

Spikelets disarticulating with attached bristles, involucres, rachis internodes, and pedicels, or rarely not disarticulating from the inflorescence.

1a. Spikelets in fascicles of 1–4, subtended by numerous bristles or enclosed by a spiny bur; inflorescence a spicate panicle.
2a. Bristles united in at least the basal ⅓, forming an indurate spiny bur ..... *Cenchrus*
2b. Bristles separated to the base, forming an involucre ..... *Pennisetum*
1b. Spikelets usually paired, not subtended by bristles nor enclosed by a spiny bur; inflorescence a raceme, panicle, or panicle of racemes.
3a. Spikelets all sessile, or rachis internodes and pedicels connate.
4a. All spikelets unisexual; staminate spikelets terminal on racemes, subsessile, chartaceous, paired; pistillate spikelets basal on racemes, solitary at each node, sunken in a hollow, cartilaginous, rachis internode ..... *Tripsacum*
4b. Spikelets either bisexual or staminate, never pistillate; staminate and pistillate spikelets paired with each other, rachis internode and pedicel united, indurate but not cartilaginous; spikelets not sunken into hollow rachis internodes.
5a. Sessile spikelet globose, the lower glume cartilaginous, strongly pitted; pedicellate spikelet chartaceous, lanceolate ..... *Hackelochloa granularis*

5b. Sessile spikelet lanceolate, the lower glume leathery or chartaceous, not pitted; pedicellate spikelet similar to sessile spikelet ..... *Hemarthria altissima*

3b. Spikelets sessile and pedicellate (pedicellate spikelet vestigial in some species but pedicel always present); rachis internodes and pedicels not connate.

6a. Inflorescence an open or contracted panicle.

7a. Pedicellate spikelets nearly identical to the sessile spikelet in form, either bisexual or pistillate.

8a. Glumes ciliate along the margins; callus hairs stiffly spreading, ¼–¾ times the length of the spikelet, brown or golden (rarely tan); panicle contracted ..... *Eriochrysis*

8b. Glumes glabrous or pubescent but not ciliate along the margins; callus hairs filiform, ¾–2 times the length of the spikelet, white; panicle open ..... *Saccharum*

7b. Pedicellate spikelets unlike the sessile spikelet in form, either staminate, vestigial, or lacking.

9a. Rachis internode and pedicel with a thin translucent line running lengthwise between 2 strong nerves; inflorescence more or less villous ..... *Bothriochloa*

9b. Rachis internode and pedicel terete or flattened but lacking a thin translucent line running lengthwise between two strong nerves; inflorescence glabrous to pubescent.

10a. Pedicellate spikelets present, staminate, equal to the sessile spikelet in length ..... *Sorghum*

10b. Pedicellate spikelets lacking although pedicel present ..... *Sorghastrum*

6b. Inflorescence of 1–several racemes (sometimes the culm freely branched at upper nodes and forming a compound panicle, but then each raceme or group of several digitate racemes subtended by a spatheate sheath).

11a. Raceme 1 per peduncle or spatheate sheath.

12a. Lower glume of sessile spikelet rugose.

13a. Pedicels and rachis internodes auriculate; margins of the lower glume of the sessile spikelet winged ..... *Coelorhachis*

13b. Pedicels and rachis internodes not auriculate; margins of the lower glume of the sessile spikelet not winged ..... *Rhytachne*

12b. Lower glume of sessile spikelet not rugose.

14a. Lower glume of the sessile spikelet sulcate between two lateral keels .. *Andropogon*

14b. Lower glume of the sessile spikelet weakly to strongly concave (rarely with a medial groove in *Schizachyrium*).

15a. Upper lemma of sessile spikelet awned (awn vestigial in some forms of *S. tenerum*) from a deeply lobed apex; lower glume of sessile spikelet acute to acuminate ..... *Schizachyrium*

15b. Upper lemma of sessile spikelet awnless; lower glume of sessile spikelet bidentate (teeth sometimes minute in *E. muticus*) ..... *Elionurus*

11b. Racemes 2–several per peduncle or spatheate sheath.

16a. Sessile spikelet with a sharp, needlelike callus and a stout twisted awn.

17a. Lower glume of pedicellate spikelet foliaceous, 6–9 mm long, distinctly 10–15-nerved, the margins membranous; sessile spikelet cartilaginous, with a longitudinal groove ..... *Agenium*

17b. Lower glume of pedicellate spikelet not foliaceous, 4–6 mm long, indistinctly 3–8-nerved, the margins firm; sessile spikelet concave, sulcate, or grooved.

18a. Upper glume of the sessile spikelet with an awn 1–5 mm long ..... *Andropogon*

18b. Upper glume of sessile spikelet awnless or with an awn less than 1 mm long ..... *Hyparrhenia*

16b. Sessile spikelet with a blunt or rounded callus, awned or awnless.

19a. Rachis internodes and pedicels with a thin, translucent line running lengthwise between 2 strong nerves; lower glume of the sessile spikelet concave or flat ..... *Bothriochloa*

19b. Rachis internodes and pedicels terete or flat, lacking a thin translucent line running lengthwise between 2 strong nerves; lower glume of sessile spikelet sulcate between 2 strong lateral keels ..... *Andropogon*

KEY IV

Disarticulation above the persistent glumes (glumes and lemmas falling in some species of *Eragrostis* but then the palea and rachilla persistent); spikelets 1–many-flowered.

1a. Lemmas bearing 3–26 awns, the awns sometimes united below to form a column but then distinctly tripartite above.

2a. Awns 10–26, not united above to form a column, stout, unequal in length ..... *Pappophorum*

2b. Awns 3, distinct or united below to form a column, slender, equal or unequal in length (rarely the lateral awns reduced and inconspicuous) ..... *Aristida*

1b. Lemmas awnless or awned, but never with 3 or more awns arising from the same lemma.

3a. Spikelets unisexual, the plants monoecious, stamens 3–6; stoloniferous aquatics or grasses of marshy soils ..... *Luziola*

3b. Spikelets bisexual; stamens 1–3; plants of various habits.
4a. Spikelets 1-flowered.
5a. Spikelets lacking a sterile rachilla internode prolonged past the base of the palea; lemma 1-nerved ..... *Sporobolus*
5b. Spikelets with a minute sterile rachilla internode prolonged past the base of the palea; lemma 1–3-nerved.
6a. Inflorescence a digitate or subdigitate whorl of 1-sided spikes 3–10 cm long; lemma 3-nerved ..... *Cynodon*
6b. Inflorescence a large, open, ovoid panicle 20–40 cm long; lemma 1-nerved ..... *Eragrostis airoides*
4b. Spikelets 2–many-flowered, with reduced florets above or below fertile floret.
7a. Spikelets dorsally compressed; florets 2, the lower floret reduced (staminate or neuter), the upper floret bisexual.
8a. Lower glume with stout, tuberculate-based, golden hairs; inflorescence a false raceme; spikelets in triads at tips of flexuous branches arranged on a central axis ..... *Loudetiopsis chrysothrix*
8b. Lower glume glabrous; inflorescence an open, branched panicle.
9a. Upper floret pubescent, 4–5 mm long, the lemma with an awn 10–20 mm long; perennial bunch grass ..... *Loudetia flammida*
9b. Upper floret glabrous, 1 2 mm long, the lemma with an awn 1–13 mm long; caespitose or with short rhizomes, but not a bunch grass; foliage cauline ..... *Arundinella hispida*
7b. Spikelets laterally compressed; florets 2–many, the lowest floret bisexual, the upper floret(s) bisexual, staminate, or neuter.
10a. Bisexual florets 3–15, all alike although the uppermost sometimes reduced or sterile.
11a. Inflorescence paniculate ..... *Eragrostis*
11b. Inflorescence a spike or a panicle of spikes.
12a. Disarticulation at the base of the lowest floret, the florets falling together as a group ..... *Dactyloctenium aegyptium*
12b. Disarticulation between the florets, the florets falling separately.
13a. Inflorescence a solitary, erect, or slightly arcuate spike ..... *Tripogon spicatus*
13b. Inflorescence composed of 2–50 spikes or spikelike racemes.
14a. Inflorescence a single (occasionally 2) whorl(s) of 3–5 spikes ..... *Eleusine indica*
14b. Inflorescence a panicle of spikes borne on an elongate axis.
15a. Glumes distinctly 3–6-nerved ..... *Gouinia*
15b. Glumes 1-nerved ..... *Leptochloa*
10b. Bisexual florets solitary (rarely 2 in *Gymnopogon*), with 1–3 reduced florets above.
16a. Inflorescence a solitary, erect spike ..... *Microchloa indica*
16b. Inflorescence of 1–several whorls of digitate or subdigitate spikes or spikelike racemes.
17a. Foliage cauline, the blades lacking a midnerve ..... *Gymnopogon*
17b. Foliage basal, or both basal and cauline, the blades with a midnerve.
18a. Plants stoloniferous perennials; upper floret absent or up to 0.5 mm long ..... *Cynodon*
18b. Plants caespitose, perennial or annual; upper florets sterile or rarely fertile, well developed, 1–2 mm long.
19a. Upper glume bilobed, lemmas dark chestnut brown; upper florets oblong or club-shaped, the lower lemma ovate or broadly elliptic, usually awnless; foliage strictly equitant ..... *Eustachys*
19b. Upper glume acute to acuminate, lemmas light brown to green; upper florets elliptic to ovate, more or less similar to the lower floret, the lower lemma usually awned; foliage not strictly equitant ..... *Chloris*

KEY V

Spikelets disarticulating below the glumes (or the glumes vestigial in *Leersia* and *Oryza*); falling singly, without attached rachis internodes or pedicels; rachis and/or panicle branches generally persistent; spikelets with 1–2 florets.

1a. Spikelets laterally compressed.
2a. Spikelets 1-flowered; lemma and palea strongly scabrous; stamens 3–6; plants usually aquatic.
3a. Spikelets with only a lemma and a palea; plants stoloniferous ..... *Leersia*
3b. Spikelets composed of 4 bracts, the fertile floret subtended by two glumelike bracts; plants caespitose or decumbent and rooting at the nodes ..... *Oryza*
2b. Spikelets 2-flowered, the lower floret staminate or neuter, the upper floret bisexual; lemma and palea glabrous or pubescent but not strongly scabrous; stamens 3; plants terrestrial.

4a. Spikelets glabrous; foliage with abundant glandular hairs giving the plants a molasseslike odor when fresh ..... *Melinis minutiflora*
4b. Spikelets pubescent; foliage glabrous or pubescent but lacking glandular, aromatic hairs.
5a. Glumes gibbous, densely pubescent, the callus densely pubescent with hairs 10–20 mm long ..... *Rhynchelytrum repens*
5b. Glumes elliptic, glabrous, the callus pubescent with hairs 1–10 mm long ..... *Arthropogon*

1b. Spikelets dorsally compressed (glumes keeled in *Ichnanthus*, *Mesosetum*, and *Oplismenus* but then the floret dorsally compressed), generally with 2 florets, the lower floret staminate or reduced, the upper floret bisexual.
6a. Spikelets paired, unequally pedicellate, the lower staminate and persistent, the upper perfect, disarticulating at the base of a pungent callus and provided with a long, stout, geniculate awn; inflorescence a solitary raceme or a conjugate pair of racemes ..... *Trachypogon plumosus*
6b. Spikelets solitary, paired, or in groups of 3 or more, but not an unequally pedicellate pair of spikelets with the lower staminate and the upper perfect, the callus never pungent, awned or awnless but the awn never geniculate; inflorescence an open panicle or of 1–many racemes.
7a. Spikelets villous, the callus hairs more than 2 times the length of the glumes, the upper lemma hyaline ..... *Imperata*
7b. Spikelets glabrous to pubescent but the hairs never more than 1.5 times the length of the spikelet, the upper lemma coriaceous to cartilaginous.
8a. Spikelets subtended by 1–10 bristles (at least apically on panicle branches); inflorescence a spicate panicle ..... *Setaria*
8b. Spikelets not subtended by bristles; inflorescence various.
9a. Spikelets with an indurate knob at base, this composed of either a swollen pedicel or the first rachilla node and the reduced, adnate lower glume.
10a. Rachis foliaceous, winged, 2–8 mm wide; spikelets paired but arranged in a single row, with the backs of the upper lemmas of adjacent spikelets facing one another ..... *Thrasya petrosa*
10b. Rachis triquetrous, 0.5–1 mm wide; spikelets paired, arranged in 2–4 regular or irregular rows, the spikelets secund or with the back of the upper lemmas facing the midrib, but not back to back ..... *Eriochloa*
9b. Spikelets lacking an indurate knob at base.
11a. Upper lemma with a laterally flattened beak or truncate scar at apex.
12a. Glumes and lower lemma glabrous; upper lemma smooth; pedicels glabrous ..... *Acroceras*
12b. Glumes and lower lemma coarsely hispid; upper lemma strongly rugose; pedicels with a ring of stout hairs at apex ..... *Brachiaria paucispicata*
11b. Upper lemma blunt or acute but not with a laterally flattened beak or truncate scar at apex.
13a. Lemma of upper floret with a pair of appendages or scars at base.
14a. Appendages composed of dense tufts of thick hairs; upper floret sessile; foliage basal, the blades linear ..... *Panicum olyroides*
14b. Appendages membranous wings or reduced to scars; upper floret on a short stipe, foliage cauline, the blades lanceolate to ovate.
15a. Inflorescence a panicle ..... *Ichnanthus*
15b. Inflorescence of 1–5 racemes arranged on a central axis; frequently spikelets with a foliaceous first glume surpassing the spikelet ..... *Echinolaena*
13b. Lemma of fertile floret lacking appendages or scars at base 16

16a. Inflorescence an open or contracted panicle.
17a. Both glumes equal in length and surpassing the floret; leaf blades with a short pseudopetiole ..... *Homolepis aturensis*
17b. Lower glume lacking or from ⅛–¾ the length of the spikelet; leaf blades with or without a pseudopetiole.
18a. Lower glume absent; spikelets densely pubescent ..... *Leptocoryphium lanatum*
18b. Lower glume present; spikelets glabrous or pubescent.
19a. Palea of the lower floret splitting when mature, the two halves becoming reflexed and the spikelets appearing winged; fertile floret brown and shining when mature ..... *Otachyrium versicolor*
19b. Palea of the lower floret not splitting, the spikelets not appearing winged; spikelets variously colored.
20a. Spikelets placed obliquely on pedicels, black at maturity, the glumes and lower lemma with tufts of hairs at apices ..... *Lasiacis*
20b. Spikelets not placed obliquely on pedicels, more or less erect, variously colored at maturity, the glumes and lower lemma glabrous or pubescent but not with tufts of hairs at apices.
21a. Inflorescence a narrow, contracted, spicate panicle.
22a. Culms pithy; upper lemma leathery, the margins flat; plants stolon-

iferous, floating aquatics or (in the dry season) rooted in the mud along the margins of streams and ponds ..... *Hymenachne*

22b. Culms hollow; upper lemma cartilaginous, the margins inrolled or flat; plants caespitose or decumbent, of humid habitats but never floating aquatics ..... *Sacciolepis*

21b. Inflorescence open or contracted, if somewhat spicate then with fewer than 25 spikelets.

23a. Spikelets inflated, subglobose; upper lemma strongly rugose; inflorescence of branched racemes with the back of the lower glume oriented towards the rachis ..... *Brachiaria*

23b. Spikelets not inflated, ovate to narrowly elliptic; upper lemma smooth (rugose in *P. maximum*); if the inflorescence somewhat racemose then spikelets neither inflated nor the lemmas rugose ..... *Panicum*

16b. Inflorescence of 1–many racemes.

24a. Spikelets subaristate to awned.

25a. Blades ovate to lanceolate, less than 3 times as long as wide; awns arising from the bidentate tips of both glumes and the lower lemma ..... *Oplismenus*

25b. Blades linear, more than 5 times as long as wide; lower glume mucronate but not awned or aristate, the upper glume and/or the lower lemma awned ..... *Echinochloa*

24b. Spikelets not awned.

26a. Inflorescence a solitary raceme.

27a. Raceme with a single row of paired spikelets oriented back to back, so that the lower glumes of each pair face each other and the upper glumes face apart; rachis foliaceous, winged ..... *Thrasya*

27b. Raceme with solitary or paired spikelets not oriented back to back; rachis winged or not.

28a. Lower glume lacking; spikelets oriented with the back of the fertile lemma towards the rachis ..... *Paspalum*

28b. Lower glume well developed; spikelets oriented with the back of the upper lemma away from the rachis.

29a. Spikelets distichous, arranged in 2 rows spreading at 180°; glumes and lower lemma pubescent with stiff, golden, or reddish hairs ..... *Mesosetum cayennensis*

29b. Spikelets secund, arranged in 2 or 4 rows but on the lower side of the rachis; glumes and lower lemma glabrous or pubescent with soft, white hairs ..... *Brachiaria*

26b. Inflorescence of 2–many conjugate, digitate, or paniculate racemes.

30a. Ligules absent; spikelets subglobose ..... *Echinochloa*

30b. Ligules present, membranous or ciliate; spikelets elliptic to subglobose.

31a. Margins of the upper lemma indurate, inrolled, clasping the back of the palea, or (rarely) the floret open.

32a. Lower glume well developed, 1–3-nerved, ¼–¾ the length of the spikelet.

33a. Spikelets narrowly elliptic, secund, irregularly arranged on short branches ..... *Panicum*

33b. Spikelets subglobose, appressed-ascending, regularly arranged in 2 or 4 rows with the back of the lower glume facing the rachis ..... *Brachiaria*

32b. Lower glume lacking or a minute nerveless scale less than ⅕ the length of the spikelet.

34a. Lower glume a minute, nerveless scale; lower floret staminate, with a well-developed palea; lemma of the upper floret not clasping the palea, the floret open ..... *Anthaenantiopsis trachystachyum*

34b. Lower glume absent; lower floret neuter, usually lacking a palea; lemma of the upper floret clasping the palea, the floret open only during anthesis.

35a. Back of the upper lemma facing away from the rachis; spikelets solitary ..... *Axonopus*

35b. Back of the upper lemma facing toward the rachis; spikelets solitary or paired ..... *Paspalum*

31b. Margins of the upper lemma hyaline, lying flat against the back of the palea.

36a. Plants floating aquatics or (in the dry season) rooted in the mud along the margins of streams and ponds, the culms solid with aerenchymous tissue; blades clasping culm; lower glume well developed ..... *Hymenachne*

36b. Plants not floating aquatics, the culms hollow; blades not clasping culm; lower glume either lacking or reduced to a small scale less than ⅕ the length of the spikelet ..... *Digitaria*

ENUMERATION OF GENERA AND SPECIES

Acroceras Stapf in Prain

Zuloaga, F. O., O. Morrone & A. A. Saénz. 1987. Estudio exomorfológico e histofoliar de las especies americanas del género *Acroceras* (Poaceae: Paniceae). Darwiniana 28(1–4): 191–217.

KEY TO SPECIES

1a. Apex of upper lemma with a stout, laterally compressed beak; pedicels ascending to appressed, borne on racemose panicle branches ..... *A. zizanioides*

1b. Apex of upper lemma with a truncate, greenish scar, not beaked; pedicels spreading, the panicle open, its branches not racemose ..... *A. excavatum*

A. excavatum (Henrard) Zuloaga & Morrone, Darwiniana 28(1–4): 195. 1987. *Panicum excavatum* Henrard, Feddes Repert. Spec. Nov. Regni Veg. 23: 179. 1926. *Lasiacis excavatum* (Henrard) L. Parodi, Notas Prelim. Mus. La Plata 8: 92. 1943.

Occasional in semideciduous forest, abundant in forest openings and logging roads; palatable (4); flowering January (*April*) to July; local name: *taquarilla*. Distribution: Venezuela, Brazil, Paraguay, and Argentina. (694, 830, 932, 967, 1001, 1740, 1891, 1966)

A. zizanioides (H.B.K.) Dandy, J. Bot. 69: 54. 1931. *P. zizanioides* H.B.K., Nov. Gen. Sp. 1: 100. 1816. *P. grandiflorum* Trin. ex Nees, Agrost. Bras. 143. 1829 (nomen nudum).

Occasional, seasonally inundated savannas and roadside ditches; flowering December to May; $2n = 36$; local name: *cañuela*. Distribution: Mexico and the West Indies to northern Argentina; Bolivia: the Beni. (689, 998, **2414**)

Actinocladum McClure

Soderstrom, T. R. 1981. Observations on a fire adapted bamboo of the Brazilian cerrado, *Actinocladum verticillatum* (Poaceae: Bambusoideae). Amer. J. Bot. 68(9): 1200–1211.

A. verticillatum (Nees) McClure ex Soderstrom, Amer. J. Bot. 68(9): 1201. 1981. *Arundinaria verticillata* Nees, Agrost. Bras. 2(1): 523. 1829. *Ludolphia verticillata* (Nees) A. Dietrich, Sp. Pl. 25. 1833. *Rhipidocladum verticillatum* (Nees) McClure, Smithson. Contr. Bot. 9: 106. 1973.

Usually reported as a *cerrado* species but in Chiquitanía it is restricted to *campo rupestre* and adjacent transitional scrub; both rhizomes and culms appear to be extremely resistant to fire; locally abundant and forming extensive colonies in Parque Nacional "Noel Kempff Mercado." Distribution: central Brazil. (1378, 2759)

Agenium Nees in Lindl.

A. villosum (Nees) Pilger, Feddes Repert. Spec. Nov. Regni Veg. 43: 82. 1938. *Heteropogon villosus* Nees, Agrost. Bras. 362. 1829. *Andropogon neesii* Kunth, Révis. Gramin. 2(39). 1832, non Trinius, 1832. *Agenium nutans* Nees in Lindl., Intr. Nat. Syst. Bot. 2: 447. 1836. *Andropogon agenium* Steudel, Syn. Pl. Glumac. 1: 395. 1854.

Rare, *cerrado*; flowering in February and March; $2n = 20$. Distribution: Brazil, Paraguay, Uruguay, and Argentina; Bolivia: Andean Piedmont of Santa Cruz. (854, **2419**)

Andropogon L.

KEY TO SPECIES

1a. Upper glume of the sessile and pedicellate spikelets aristate.
  2a. Racemes 1/peduncle; upper glume of pedicellate spikelet enlarged and winglike; caespitose annuals ..... *A. fastigiatus*
  2b. Racemes 2/peduncle; upper glume of pedicellate spikelet not winglike; perennial bunch grasses.
    3a. Callus of sessile spikelet pungent; culms slender, 1–2 mm in diameter; rachis internodes and pedicels 0.5–0.8 mm wide at the apex ..... *A. angustatus*
    3b. Callus of sessile spikelet blunt; culms 3–5 mm in diameter; rachis internodes and pedicels 1–1.5 mm wide at the apex ..... *A. gayanus*

1b. Upper glume of sessile and pedicellate spikelets acuminate, acute, or minutely bidentate (subaristate in the pedicellate spikelet of *A. sanlorenzanus*).
  4a. Culm abundantly branched at upper nodes to form a corymbose or elongate compound panicle of numerous (more than 30) spatheate inflorescences, each bearing 1–2(3) included or scarcely exserted racemes.

5a. Racemes 1/spatheate inflorescence; pedicellate spikelet well developed and staminate at all the nodes of the raceme.
6a. Rachis internodes and pedicels ciliate; sessile spikelet bisexual ..... *A. insolitus*
6b. Rachis internodes and pedicels glabrous; sessile spikelet pistillate ..... *A. virgatus*
5b. Racemes 2 3/spatheate inflorescence; pedicellate spikelet staminate at terminal rachis nodes but vestigial below.
7a. Sessile spikelets awnless; racemes straight; panicles corymbose ..... *A. bicornis*
7b. Sessile spikelets awned; racemes flexuous; panicles elongate ..... *A. glaziovii*
4b. Culms branched or unbranched but not forming a compound panicle; racemes (2)3–6 per sheath, digitate; if inflorescences numerous (10–25 in some variants of *A. lateralis*) then clearly exserted.
8a. Pedicellate spikelets well developed, subequaling or surpassing the sessile spikelet in length.
9a. Culms freely branched at the middle and upper nodes, 150–200 cm tall, 5–30 inflorescences/culm ..... *A. lateralis*
9b. Culms unbranched or sparsely branched, 30–40 cm tall, 1–3 inflorescences/culm.
10a. Sessile spikelet awnless, 5–5.5 mm long; racemes 4–6/peduncle; culms with 2–3 inflorescences borne at the upper nodes; pedicellate spikelets staminate, 6 mm long ..... *A. sanlorenzanus*
10b. Sessile spikelet awned, 4–4.5 mm long; racemes 3 per peduncle; culms unbranched, bearing a single terminal inflorescence; pedicellate spikelets neuter (rarely staminate), 3–4 mm long ..... *A. carinatus*
8b. Pedicellate spikelets vestigial, up to ¼ the length of the sessile spikelet.
11a. Sessile spikelets awned; rachis hairs equaling the sessile spikelet; mature culms with a single, terminal inflorescence ..... *A. macrothrix*
11b. Sessile spikelets awnless; rachis hairs twice the length of the sessile spikelet; mature culms with 2–3 terminal and axillary inflorescences.
12a. Racemes 3–5; leaf blades 3–5 mm wide, carinate at apex; spikelets 3–5 mm long; plants loosely caespitose, the culms somewhat geniculate ..... *A. selloanus*
12b. Racemes 2–3; leaf blades 1–3 mm wide, acuminate; spikelets 2.5–3.5 mm long; plants densely caespitose, the culms erect ..... *A. leucostachyus*

A. angustatus (C. Presl) Steudel, Syn. Pl. Glumac. 1: 370. 1854. *Diectomis laxa* Nees, Agrost. Bras. 340. 1829, non *A. laxus* Willd., 1806. *D. angustata* C. Presl, Rel. Haenk. 1: 333. 1830.

Occasional, seasonally humid savanna and in white sandy soils on valley-side *campos* (upslope); flowering February to (*April*) May; meiosis abnormal, plants probably apomictic. Distribution: Mexico and the West Indies to Brazil. (886, 960, 2078, 2459)

A. bicornis L., Sp. Pl. 1046. 1753.

Occurring in a wide range of natural and disturbed habitats; occasional in seasonally inundated savannas, *cerrado*, and forest margins; abundant in old fields and along most roadsides in savanna and forest soils; unpalatable (2); flowering November to (*January* to *March*) May. Distribution: Mexico to Argentina; Bolivia: Andean Piedmont of Santa Cruz, Cochabamba, Beni, and the Yungas. (626, 672, 682, 1555)

A. carinatus Nees, Agrost. Bras. 2: 330. 1829. *A. carinatus* var. *leiophyllus* Hack. in A. DC., Monogr. Phan. 6: 434. 1889, *A. carinatus* var. *exserens* Hack. in Mart., Fl. Bras. 2(3): 288. 1883.

Poorly represented in herbaria but locally abundant in *campo rupestre* on Serranía de Santiago; flowering is dependent upon fire. Distribution: Costa Rica and Brazil. (2790)

A. fastigiatus Sw., Prodr. 26. 1786. *Diectomis fastigiata* (Sw.) P. Beauv., Ess. Agrostogr. 132: 160. 1812.

Occasional, in superficial soils on lateritic crests and granitic outcrops, locally abundant as a weed along road embankments in savanna soils; flowering November to (*April*) May; $2n = 20$. Distribution: throughout the tropics. (800, 1511, 1853, 2019, **2395**)

A. gayanus Kunth, Révis. Gramin. 1: 163. 1829.

Cultivated forage grass of recent introduction by the British Mission in Tropical Agriculture (Patterson, 1984), usage not widespread; two different populations observed to flower in November and April. (1409A, 1964)

A. glaziovii Hack. in Mart., Fl. Bras. 2(3): 286. 1883.

Poorly represented in herbaria but abundant in Chiquitanía, codominant with *Saccharum trinii* and *Arundinella hispida* in savanna marsh; coarse and

unpalatable (0); flowering in *May* and June. Distribution: central Brazil. (983, 2031, 2082)

A. insolitus Sohns, Mem. New York Bot. Gard. 9(3): 271. 1957.

Closely related to *A. virgatus* from which it is distinguished by ciliate pedicels and rachis internodes, more elongate racemes, and a bisexual sessile spikelet; reminiscent of *A. bicornis* and *Schizachyrium microstachyum*. Rare, savanna marsh; flowering in April. Distribution: Venezuela and Brazil; only the fifth known collection. (*Killeen 2484*; additional specimens examined: VENEZUELA: *Maguire & Wurdack 3577* US, NY; *Davidse & González 12710* MO. BRAZIL: *Harley et al. 15771* MO; *Irwin 8734* US)

A. lateralis Nees, Agrost. Bras. 329. 1829. *A. brevis* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 2: 268. 1832. *A. glaucescens* var. *lateralis* (Nees) Hack. in Mart., Fl. Bras. 2(3): 289. 1883. *A. incanus* Hack. in A. DC., Monogr. Phan. 6: 432. 1889.

Populations vary in stature, size of the sessile spikelet (3–5 mm), pedicellate spikelet (4–8 mm), and the length of the awn of the sessile spikelet. Closely related taxa of doubtful status are *A. hypogynus* Hack. (racemes 4–10), *A. coloratus* Hack. (awnless), *A. herzogii* Hack. (rachis and pedicels glabrous), and *A. lindmanii* Hack. ex Lindman (rachis and pedicels densely villous). This species is common in the sandy soils of seasonally humid savannas around San Ignacio de Velasco but is completely lacking from *cerrado* communities near Concepción, Lomerío, and San Javier, which are generally characterized by clay or sandy clay soils. Plants flower from August to January and blooming is possibly stimulated by fire. Distribution: Brazil, Paraguay, Argentina and Uruguay; Bolivia: Andean Piedmont of Santa Cruz and the Beni. (754, 1114, 1246, 1550, 1662, 2295, 2819)

A. leucostachyus H.B.K., Nov. Gen. Sp. 1: 187. 1816. *A. lanuginosa* H.B.K., Nov. Gen. Sp. 1: 187. 1816.

Rare in Chiquitanía, as a weed of pastures, disturbed savannas, and roadsides; flowering is stimulated by fire. Distribution: Mexico and the West Indies to Argentina; Bolivia: Andean Piedmont of Santa Cruz, Beni, and the Yungas. (1255, 1275, 1359, 1502, 2292, 2816; *Thomas 5651* NY, LPB)

A. macrothrix Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 2: 270. 1832. *A. ternatus* subsp. *macrothrix* (Trin.) Hack. in Mart., Fl. Bras. 2(3): 287. 1883.

Similar to *A. ternatus* (Sprengel) Nees, which has fewer racemes (3 vs. 4–6), larger spikelets (5–6 mm vs. 4–5 mm), longer awns (2–2.5 cm vs. 1.5–2 mm), and more densely villous rachis internodes and pedicels. Rare, valley-side *campo* (midslope); flowering is stimulated by fire. Distribution: Brazil, Uruguay, and Argentina. (1869, 2195)

A. sanlorenzanus Killeen, sp. nov. TYPE: Serranía de San Lorenzo, 10 km W of San Javier, Prva. Ñuflo de Chávez, Dpto. Santa Cruz, Bolivia (16°15′S, 62°40′W), 800–900 m, 30 Oct. 1987, *Killeen 2832* (holotype, ISC; isotypes, LPB, F, MO, US, SI). Figure 2.

A. carinatus Nees, affinis sed culmis 3–4 nodis, ramosis superne a 2–3 paniculis racemorum; racemis 3–5; basibus glumarum sulcatis valde, carinis ad medium contingentibus, carinis uninervibus; aristis vestigialibus apicem lemmatum 1.0–1.5 mm longis, nonexcurrentibus, spiculis muticis apparenter; spiculis pedicellatis 5.5–6.0 mm longis notabilis.

Caespitose, perennial bunch grass; culm glabrous, 30 cm tall, with 2–5 nodes visible above the basal foliage. Sheaths keeled, glabrous, strongly nerved, the margins membranous; ligules membranous, 0.2 mm long; blades broadest at base, equaling the sheath in width, folded, revolute when stressed, the adaxial surface glabrous with a thickened midrib, the abaxial surface pilose with an indistinct midnerve, 1–13 cm long, 2.4 cm wide (folded), reduced at the upper nodes. Inflorescences 2–3, terminal and axillary, inserted at the upper nodes, each composed of 4–6 digitate racemes 3–6 cm long; spikelets paired, sessile and pedicellate; rachis internodes 3 mm long, flattened, with cilia 2.5–3 mm long; pedicels similar, united with the sessile spikelet and the rachis internode at the base to form a bearded callus, the hairs 2 mm long; disarticulation below the glumes, the sessile spikelets falling attached to the rachis internodes and pedicels, the pedicellate spikelets falling separately. Sessile spikelets bisexual, 5 mm long; lower glume 5 mm long, bicarinate, the midnerve suppressed, each of the 2 keels composed of a single ridgelike nerve, strongly sulcate with the 2 keels reflexed and touching in the middle; upper glume 5 mm long, laterally compressed; lower lemma hyaline, 4.5–5 mm long, similar to the lower glume in form, ciliate on the margins, the lower palea lacking;

FIGURE 2. *Andropogon sanlorenzanus* (*Killeen 2832*).—A. Habit (bar = 5 cm).—B. Sessile and pedicellate spikelet pair.—C. Lower glume of the sessile spikelet (B and C: bar = 1 mm).

upper lemma 3.4 mm long, hyaline, with a vestigial awn 1.5 mm long arising between the 2 lobes, not exserted from the spikelets and only visible upon dissection, the palea minute; stamens 3, the anthers 2 mm long, yellow; lodicules truncate, fleshy. Pedicellate spikelet staminate, 5.5–6 mm long; lower glume as long as the spikelet, dorsally compressed, lanceolate, acuminate, chartaceous, 7-nerved, the midnerve distinct, the lateral nerves submarginal; upper glume somewhat subequaling the spikelet, laterally compressed, lanceolate, acuminate, membranous, 1(3)-nerved; lower lemma 4 mm long, hyaline, lanceolate; upper lemma 4 mm long, hyaline, lanceolate, ciliate on the margins, the palea 1.5 mm long, erose; stamens 3, the anthers 2.5 mm long, yellow.

This species is locally abundant in *campo rupestre* vegetation; flowering depends upon fire as the locality was visited on several occasions throughout the year and only those patches of savanna burned three to five weeks previously contained blooming individuals. The new species is similar to *A. carinatus* in life form, foliage, phenology, and habitat, but in *A. sanlorenzanus* the culm is branched to produce 2–3 (vs. 1) inflorescences, each with 4–6 (vs. 3) racemes, the sessile spikelet is 5–5.5 mm (vs. 4–4.5 mm) long, the awn of the upper lemma of the sessile spikelet is vestigial (vs. well developed), and the staminate pedicellate spikelet is 6 mm long (vs. neuter or rarely staminate and 3–4 mm long). Although collections are not numerous, these two species appear to be part of a variable complex in which widely separated and isolated populations have undergone considerable divergence.

A. selloanus (Hack.) Hack., Bull. Herb. Boissier, Sér. 2. 4: 266. 1904. *A. leuchostachyus* subsp. *selloanus* Hack. in A. DC., Monogr. Phan. 6: 420. 1889.

This species is widely distributed in natural savanna habitats with a range of water economies, from permanently humid savanna marsh to xeric gravel soils in *cerrado*, but it is zonally abundant as a codominant with *Paspalum stellatum* and *P. lineare* on valley-side *campos* (upslope); palatable (3); stimulated by fire, although populations also flower irregularly throughout the year. Distribution: Mexico and the West Indies to Argentina; Bolivia: the Andean Piedmont of Santa Cruz and the Beni. (522, 530, 577, 627, 709, 760, 1242, 1348, 1581, 1790, 1836, 2171, 2205, 2221, 2224, 2816)

A. virgatus Desv. in Ham., Prodr. Pl. Ind. Occ. 9. 1825. *Hypogynium virgatus* (Desv.) Dandy, J. Bot. 69: 54. 1931. *H. spathiflorum* Nees, Agrost. Bras. 366. 1829. *A. spathiflorus* (Nees) Kunth, Enum. Pl. 1: 496. 1833.

The common variant of this species has contracted, corymbose, compound panicles with included peduncles; flowering in these populations is unaffected or retarded by fire. However, occasional populations have open, elongate compound panicles with exserted peduncles (2771, 2775); fire-stimulated flowering in these populations. Common, valley-side *campo*, seasonally inundated savanna, savanna marsh, and seasonal ponds; somewhat palatable (2); flowering November to (*January*, *February*, *March*) May; $2n = 20$. Distribution: Central America and the West Indies to northern Argentina; Bolivia: the Andean Piedmont of Santa Cruz and the Beni. (621, 625, 731, 1591, 1746, 1858, **2420**, 2771, 2775)

Anthaenantiopsis Mez

A. trachystachyum (Nees) Mez, Bot. Jahrb. Syst. 56(125): 11. 1921. *Panicum trachystachyum* Nees, Agrost. Bras. 125. 1829.

Locally abundant in *campo cerrado* with Chacoan influences 10 km N of Roboré; flowering depends upon fire. Distribution: Brazil and Paraguay. (2780)

Aristida L.

Henrard, J. T. 1926, 1927, 1928, 1933. "A Critical Revision of the genus *Aristida*." Meded. Rijks-Herb. 54(3 vols. & suppl.): 1–747. Henrard, J. T. 1929, 1932. "A monograph of the genus *Aristida*." Meded. Rijks-Herb. 58(2 vols.): 1–325. Caro, J. A. 1961. Las especies de *Aristida* (Gramineae) del centro de la República Argentina. Kurtziana 1: 123–206.

KEY TO SPECIES

1a. Margins of lemma inrolled on lower ½, the floret grooved on the ventral surface.
  2a. Column less than 1 mm long, not twisted, the lemma grooved throughout; awns ascending.
    3a. Glumes equal to or surpassing the lemma (inclusive of column), acuminate or bidentate *A. circinalis*
    3b. Glumes ½–¾ the length of the lemma (inclusive of column), blunt ..... *A. succedeana*
  2b. Column 1–15 mm, twisted, only the lower ½ of lemma grooved; awns ascending, recurved or spiral.
    4a. Column 10–15 mm long in mature specimens, separated from the lemma by an articulation point; awns spirally coiled; caespitose perennial bunch grass with long (to 1 m) setaceous leaf blades ..... *A. macrophylla*
    4b. Column 1–3 mm long in mature specimens, articulation point absent (rarely present in some forms of *A. hassleri*); awns ascending or recurved; caespitose perennials, but not bunch grasses, the leaf blades 20–30 cm long, not setaceous.
      5a. Awns equal or subequal, recurved; leaf blades spirally coiled when senescent ..... *A. hassleri*

5b. Lateral awns ½–⅔ the length of central awn, ascending; leaf blades not spirally coiled ..... *A. gibbosa*

1b. Margins of the lemma overlapping, the floret not grooved on the ventral surface.
6a. Column 10–35 mm long.
7a. Callus bidentate ..... *A. riparia*
7b. Callus not bidentate ..... *A. megapotamica*
6b. Column absent or up to 5 mm long.
8a. Lower glume much longer than and obscuring the upper glume; foliage cauline ..... *A. mendocina*
8b. Lower glume less than or equal to the upper glume, rarely slightly longer; foliage basal or cauline.
9a. Awns 7–10 cm long, filiform, purple; lower glume with 5 distinct nerves ..... *A. venustula*
9b. Awns 0.5–3 cm long; lower glume 1–(3)-nerved.
10a. Lateral awns equal or nearly equal to the central awn.
11a. Awns distinctly spirally coiled; caespitose perennials, the culms 30–50 cm tall, sparsely branched ..... *A. recurvata*
11b. Awns spreading to ascending; caespitose annuals, the culms 10–20 cm tall, freely branched ..... *A. capillacea*
10b. Lateral awns ½–⅔ the length of central awn.
12a. Central awn arcuate, forming a half circle; panicles loosely contracted ..... *A. torta*
12b. Central awn ascending, not arcuate; panicles open, lax ..... *A. longifolia*

A. capillacea Lam., Tabl. Encycl. 1: 156. 1791. *A. elegans* Rudge, Pl. Guian. 22. t. 30. 1805.

Occasional, in white sandy soil of valley-side *campos* (upslope) and superficial soil on granitic outcrops; growth is restricted to the dry season in seasonally humid habitats with exposed soil; flowering May to October. Distribution: Mexico to Argentina; Bolivia: Andean Piedmont of Santa Cruz, Beni, and the Yungas. (958, 1130, 1249, 2107)

A. circinalis Lindman, Köngl. Svenska Vetenska Acad. Handl. 34(6): 13. 1900. *A. leptochaeta* Hack., Feddes Repert. Spec. Nov. Regni Veg. 6: 344. 1909. *A. rosacea* Mez, Feddes Repert. Spec. Nov. Regni Veg. 17: 151. 1921.

Similar to and possibly not distinct from *A. succedeana* Henrard and *A. aristiglumis* Caro. Rare in sandy soils near Roberé; flowering is apparently stimulated by (but not dependent upon) fire; August to January. Distribution: Argentina, Paraguay, and Uruguay; Bolivia: Andean Piedmont of Santa Cruz, Gran Chaco, and the Yungas. (740, 1120, 1243, 1278, 1544, 1569, 2809)

A. gibbosa (Nees) Kunth, Enum. Pl. 1(1): 189. 1833. *Chaetaria gibbosa* Nees, Agrost. Bras. 383. 1829.

Rare, superficial soils on granitic outcrops in *campo rupestre* on Serranía de San Lorenzo; flowering in April. Distribution: central Brazil. (1979)

A. hassleri Hack., Bull. Herb. Boissier, Sér. 2, 4(3): 277. 1904. *A. longiramea* Presl. var. *boliviana* Henrard, Meded. Rijks-Herb. 40: 56. 1921. *A. hassleri* Hack. var. *aculeolata* Hack., Feddes Repert. Spec. Nov. Regni Veg. 7: 373. 1909.

Rare, superficial soils over granitic outcrops; unpalatable (0); flowering November to January. Distribution: Paraguay. (820, 1221, 1544)

A. longifolia Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 1: 84. 1831. *A. bromoides* Salz. ex Trin. & Rupr., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 7(1): 118. 1842, non H.B.K., 1816.

Rare, sandy soils in *cerrado* (Santiago de Chiquitos) and the Gran Chaco; flowering in May. Distribution: Venezuela, Colombia, and Brazil; Bolivia: the Beni. (1271, 2783)

A. macrophylla Hack., Denkschr. Kaiserl. Akad. Wiss. Math. Naturwiss. Kl. 79: 16. 1906. *A. subarticulata* Mez, Feddes Repert. Spec. Nov. Regni Veg. 17: 148. 1921.

Henrard (1927) cited *A. hassleri* var. *aculeolata* Hack. as a synonym based on the presence of an articulation point at the apex of the lemma; however, the type specimen (*Hassler 9849*, fragment US) has spikelets with reflexed rather than contorted awns and is better treated as a variety of *A. hassleri* Hack. Henrard (1927) also cited *A. endomellas* Mez as a synonym of *A. macrophylla* but the type (*Hassler 11323*, fragment US) lacks both an articulation point and contorted awns. Common in *cerrado*; the foliage is coarse and unpalatable (0); flowering January to (*February*) April;

$2n = 22$. Distribution: central Brazil. (794, 852, 1805, 1841, 1893, 1995, **2392**)

A. megapotamica Spreng., Syst. Veg. 16(4): 31. 1827. *A. implexa* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 4(1): 48. 1836. *A. paraguayensis* Lindman, Köngl. Svenska Vetensk. Akad. Handl. 34(6): 14. 1900. *A. sellowii* Mez, Feddes Repert. Spec. Nov. Regni Veg. 17: 148. 1921.

Not yet collected in Chiquitanía; rare in sandy well-drained soils of the Andean Piedmont of Santa Cruz; flowering in January. Distribution: Brazil, Paraguay, Uruguay, and Argentina. (1562)

A. mendocina Philippi, Anales Univ. Chile 36: 205. 1870. *A. cordobensis* Hack. in Stuck., Anales Mus. Nac. Hist. Nat. Buenos Aires 11: 91. 1904. *A. inversa* Hack. in Fries, Ark. Bot. 8: 37. 1908. *A. mendocina* var. *macrantha* (Parodi) Henrard, Meded. Rijks-Herb. 54a: 267. 1927.

Rare, in sandy soils; unpalatable (0); flowering from January to August. Distribution: Argentina and Chile; Bolivia: Andean Piedmont of Santa Cruz, where it is commonly found as a colonizer on sand dunes. (927, 1042, 1119, 1265, 1272, 1570, 1726, 2500)

A. recurvata H.B.K., Nov. Gen. Sp. 1: 123. 1816. *A. riedeliana* Trin. & Rupr., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 7(1): 113. 1842. *A. neesiana* Trin. & Rupr., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 7(1): 113. 1842.

Occasional, gravel soils and lateritic crests in *cerrado*; unpalatable (0); flowering April to July. Distribution: Central America, Venezuela, and Brazil. (907, 1019, 1907, 2008, 2049, 2097)

A. riparia Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 6: 48. 1836. *A. implexa* var. *aequa* Trin. & Rupr., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 7: 124. 1842.

Common, in *cerrado* and *campo rupestre*; the foliage is coarse and shows no evidence of selective grazing, but the species is less abundant in overgrazed savannas, unpalatable (1–2); flowering January to (*April*) June; $2n = 22$. Distribution: Venezuela, the Guianas, Brazil, and Paraguay; Bolivia: the Yungas. (697, 726, 759, 910, 1168, 1830, 1837, 1954, 1983, 2000, 2016, 2060, **2422**)

A. succedeana Henrard, Med. Rijks-Herb. 58A: 294, pl. 144. 1932.

Common, *cerrado*; unpalatable (0) except after being burned; flowering is stimulated but not dependent upon fire, August to January; $2n = 22$. Distribution: central Brazil. (545, 1103, 1167, 1193, 1367, 1558, 2115, **2242**, 2778)

A. torta (Nees) Kunth, Révis. Gramin. 1: 190. 1830. *Chaetaria torta* Nees, Agrost. Bras. 386. 1829. *A. spadicea* sensu Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 4(1): 43. 1836, auct. non H.B.K., 1816. *A. tincta* Trin. & Rupr., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 7(1): 111. 1842. *A. breviglumis* Mez, Feddes Repert. Spec. Nov. Regni Veg. 17: 152. 1921.

Not yet collected in Chiquitanía but common along trails in shallowly inundated savannas in the Beni. Distribution: Venezuela, the Guianas, and Brazil. (2602)

A. venustula Arechav., Anales Mus. Nac. Montevideo 4(1): 77. 1902. *Chaetaria pallens* var. *tenuifolia* Nees, Agrost. Bras. 381. 1829. *A. pallens* var. *tenuifolia* (Nees) Trin. et Rupr., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 7(1): 116. 1842. *A. pallens* var. *genuina* f. *breviaristata* Hack., Anales Mus. Nac. Hist. Nat. Buenos Aires 21: 69. 1911.

Not yet collected in Chiquitanía; flowering is stimulated by fire. Distribution: Brazil, Paraguay, Uruguay, and Argentina; Bolivia: Andean Piedmont of Santa Cruz. (1240)

Arthropogon Nees

Filgueras, T. S. 1982. Taxonomia e distribucão de *Arthropogon* Nees (Gramineae). Bradea 3(36): 303–322.

KEY TO SPECIES

1a. Callus hairs 2–4 mm long; lower glume 0–10 mm long (including awn); panicle pyramidal ..... *A. villosus*

1b. Callus hairs 0.5–1 mm long; lower glume 10–18 mm long (including awn); panicle narrowly elliptic ..... *A. scaber*

A. scaber Pilger & Kuhlm. in Kuhlm., Comiss. Linhas Telegr. Estratég. Mato Grosso Amazonas 67, Annexo 5, Bot. 11: 37. 1922. *A. bolivianus* Filgueiras, Brittonia 38(1): 71. 1986.

Rare, Santiago de Chiquitos. Distribution: central Brazil. (Cutler 7023)

A. villosus Nees, Agrost. Bras. 319. 1829. *A. villosus* Nees var. *glabrescens* S. Moore, Trans. Linn. Soc. London, Bot. 4: 508. 1895.

Uncommon, forming lawnlike colonies in *cerrado*, locally abundant in the hill region SE of San Javier; palatable (3); flowering is dependent upon fire. Distribution: central Brazil. (1112, 1178)

Arundinella Raddi

A. hispida (Willd.) Kuntze, Revis. Gen. Pl. 2: 761. 1891. *Andropogon hispidus* Humb. & Bonpl. ex Willd., Sp. Pl. 4: 908. 1806. *Goldbachia mikanii* Trin. in Sprengel, Neue Entdeck 2: 42. 1821. *Arundinella brasiliensis* Raddi, Agrost. Bras. 37. 1823. *Piptatheria confine* Schultes, Mant. 2: 184. 1824. *A. mikanii* (Trin.) Nees, Agrost. Bras. 465. 1829. *A. confinis* (Schultes) Hitchc. & Chase, Contr. U.S. Natl. Herb. 18: 290. 1917.

Abundant as a codominant of savanna marsh with *Saccharum trinii*, occasionally in seasonally inundated savanna and valley-side *campo* (downslope), and a single population (2096) was collected in well-drained soils on a *cerrado*/forest margin; flowering January to (*May*) July. Distribution: Mexico to Argentina; Bolivia: Andean Piedmont of Santa Cruz and the Beni. (843, 920, 980, 1593, 2021, 2038, 2088, 2096, 2593)

Arundo L.

A. donax L., Sp. Pl. 81. 1753.

Cultivated in Roboré for ornament and, presumably, roof construction.

Axonopus P. Beauv.

Black, G. A. 1963. Grasses of the genus *Axonopus* (a taxonomic treatment). L. B. Smith (editor), Advancing Frontiers of Plant Sciences 5: 1–186. Garófalo-Spalding, B. 1988. Systematics of the genus *Axonopus* section *Cabrera* (Gramineae, Paniceae). Masters Thesis, Iowa State Univ., Ames, Iowa.

KEY TO SPECIES

1a. Rachis pubescent with papillose-based hairs.
  2a. Rachis hairs white, softly pilose or a mixture of many white hairs with a few stout golden hairs subtending spikelets.
    3a. Spikelets 2–2.5 mm long, appressed to rachis, at least some subtended by a few golden hairs ..... *A. herzogii*
    3b. Spikelets 3–5 mm long, divergent from rachis, goden hairs absent ..... *A. brasiliensis*
  2b. Rachis hairs golden, stout; white hairs absent.
    4a. Spikelets sunken into cavities of a thickened rachis 0.8–1.5 mm wide; apex of rachis prolonged, naked ..... *A. chrysoblepharis*
    4b. Spikelets not sunken in cavities, the rachis 0.4–0.7 mm wide, bearing spikelets to the apex.
      5a. Spikelets glabrous, 1.2–1.4 mm long ..... *A. exasperatus*
      5b. Spikelets pubescent, 1.2–2.0 mm long.
        6a. Spikelets 1.6–2.0 mm long; racemes 4–7 mm long; leaf blades 4–6 mm wide and 8–14 cm long ..... *A. canescens*
        6b. Spikelets 1.3–1.7 mm long; racemes 8–12 mm long; leaf blades 2–3 mm wide and 4–8 cm long ..... *A. pulcher*
1b. Rachis scabrous or glabrous, lacking papillose-based hairs.
  7a. Midnerve of glume and lower lemma distinct; leaf blades involute and setaceous-tipped; robust caespitose bunch grasses ..... *A. barbigerus*
  7b. Midnerve of glume and lower lemma suppressed (if developed, then weak when compared with lateral nerves); foliage usually compressed; never robust bunch grasses, often stoloniferous.
    8a. Upper floret brown.
      9a. Racemes 5–10 cm long; glume and lower lemma equaling the upper floret ..... *A. cuatrecasasii*
      9b. Racemes 15–30 cm long; glume and lower lemma surpassing the upper floret by 0.5–1 mm.
        10a. Innovations extravaginal; upper lemma with a tuft of white hairs at apex ..... *A. paranaensis*
        10b. Innovations intravaginal; upper lemma glabrous at apex ..... *A. leptostachyus*
    8b. Upper floret stramineous.
      11a. Glume and lower lemma with stiff marginal hairs; spikelets 2.5–3 mm long ..... *A. marginatus*
      11b. Glume and lower lemma glabrous or sparsely pilose, the hairs not stiff; spikelets 1.5–2 mm long.
        12a. Leaf blades linear-lanceolate, 5–10 mm wide, flat, not folded ..... *A. compressus*
        12b. Leaf blades linear, 2–3(–5) mm wide, folded ..... *A. fissifolius*

A. barbigerus (Kunth) Hitchc. & Chase, Contr. U.S. Natl. Herb. 24: 433. 1947. *Paspalum barbatum* Nees ex Trin., Sp. Gram. 1(9): 98. 1827, non Schultes, 1827. *P. barbigerum* Kunth, Révis. Gramin. 1: 24. 1829. *A. barbatus* (Nees ex Trin.) Kuhlm., Comiss. Linhas Telegr. Estratég. Mato Grosso Amazonas 67, Annexo 5, Bot. 11: 45. 1922. *A. eminens* var. *bolivianus* G. A. Black, Adv. Frontiers Pl. Sci. 5: 93. 1963. *A. pilosus* G. A. Black, Adv. Frontiers Pl. Sci. 5: 100. 1963. *A. perlongus* G. A. Black, Adv. Frontiers Pl. Sci. 5: 89. 1963.

This grass is part of a species complex, which includes *A. siccus* (Nees) Kuhlm., which is less robust and had smaller inflorescences, *A. eminens* (Nees) G. A. Black, which has wider (1.5 cm) leaf blades, and *A. pellitus* (Nees ex Trin.) Hitchc. & Chase, which is characterized by densely hirsute foliage. Populations in Chiquitanía vary for nodal pubescence, foliage scabrosity, length of blades, and inflorescence morphology; however, spikelet morphology is uniform for all populations sampled. An important constituent of *campo rupestre*, *cerrado*, *cerrado scrub*, seasonally inundated savanna, and valley-side *campos*; foliage is coarse and unpalatable (0). In general, plants in well-drained sites had longer, setaceous-tipped blades and flower later than populations growing in savanna wetland habitats. However, differences were not sufficient nor consistent enough to justify recognition of two separate taxa. All plants sampled had very low seed set (about 3%, 12 individual plants sampled in 3 populations) even though meiosis and pollen development appeared entirely normal. Populations in savanna wetlands flower October (*December*) to February, while populations in well-drained habitats bloom February (*March*) to May; $2n = 20$. Distribution: Brazil, Paraguay, Uruguay, and Argentina; Bolivia: Andean Piedmont and montane tropical savannas of Santa Cruz and the Beni. (705, 723, 753, 1501, 1518, 1663, 1839, 1976, 1986, **2266, 2267,** 2381, **2399**)

A. brasiliensis (Sprengel) Kuhlm., Comiss. Linhas Telegr. Estratég. Mato Grosso Amazonas 67, Annexo 5, Bot. 11: 47. 1922. *Eriochloa brasiliensis* Sprengel, Syst. Veg. 1: 249. 1825. *Paspalum dissitiflorum* Trin., Gram. Panic. 92. 1826. *Lappagopsis bijuga* Steudel, Syn. Pl. Glumac. 1: 112. 1854. *P. brasiliense* (Sprengel) Hack., Ergebn. Bot. Exped. Akad. Wiss. Sudbras. 7. 1906. *A. bijugus* (Steudel) Chase, Proc. Biol. Soc. Wash. 24: 136. 1911. *A. dissitiflorus* (Trin.) Chase, Proc. Biol. Soc. Wash. 24: 235. 1911.

Common, in *campo rupestre*; flowering is dependent upon fire. Distribution: Brazil and Paraguay. (1402, 2788, 2834)

A. canescens (Nees in Trin.) Pilger, Engl. & Prantl, Nat. Pflanzenf. ed. 2. 14: 55. 1940. *Paspalum canescens* Nees in Trin., Gram. Panic. 2: 89. 1826. *Panicum chrysodactylon* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 3(2): 197. 1835. *A. chrysodactylon* (Trin.) Kulhm., Comiss. Linhas Telegr. Estratég. Mato Grosso Amazonas 67, Annexo 5, Bot. pt. 11: 48. 1922.

Rare, in *cerrado* of hill region SE of San Javier; flowering in *March*. Distribution: Venezuela, Colombia, and Brazil. (2383)

A. chrysoblepharis (Lag.) Chase, Proc. Biol. Soc. Wash. 24: 134. 1911. *Paspalum aureum* H.B.K., Nov. Gen. Sp. 1: 93, p. 27. 1816. *Cabrera chrysoblepharis* Lag., Gen. Sp. Pl. 5. 1816. *Digitaria aurea* Sprengel, Syst. Veg. 1: 272. 1825. *P. savannarum* Schlecht., Linnaea 26: 132. 1853. *P. chrysoblephare* (Lag.) Doell in Mart., Fl. Bras. 2(2): 114. 1877. *A. aureus* var. *pilosus* (Doell) Henrard, Blumea 4: 510. 1941.

A similar species, *A. excavatum* (Nees ex Trin.) Henrard, is an annual. Common, a characteristic species of *campo cerrado* where it grows in open spaces between large bunch grasses; unpalatable (0); flowering February to (*April*) May; $2n = 20$. Distribution: Central America to Paraguay; Bolivia: Andean Piedmont of Santa Cruz, Beni, and the Yungas. (874, 894, **1849,** 1957, 1992, 2011A, 2113, **2456,** 2591)

A. compressus (Sw.) P. Beauv., Ess. Agrostogr. 154. 1812. *Milium compressum* Sw., Prod. Veg. Ind. Occ. 24. 1788. *Paspalum platycaulon* Poir. ex Lam., Encycl. Suppl. 5: 34. 1804; see Black (1963) for a complete synonymy.

Common, as a weed of pastures and roadsides; occasionally forming colonies on forest/savanna margins; foliage palatable and resistant to trampling by cattle but unproductive and of limited value as a forage resource; flowering November to June. Distribution: throughout the tropics. (556, 652, 968, 1058, 1680, 1751)

A. cuatrecasasii G. A. Black, Adv. Front. Pl. Sci. 5: 147. 1963.

Rare in Chiquitanía but common on the Andean Piedmont in sandy, well-drained savanna and scrub, often colonizing dunes; flowering January to May. Distribution: Venezuela and Colombia. (928, 1123, 1577, 1725, 2290)

A. exasperatus (Nees) G. A. Black, Adv. Front. Pl. Sci. 5: 168. 1963. *Paspalum aureum* sensu Trin., Sp. Gram. 1(9): 97. 1828, auct. non H.B.K., 1816. *Paspalum exasperatum* Nees, Agrost. Bras. 81. 1829, non *Panicum exasperatum* Nees ex Steudel, Syn. Pl. Glumac. 1: 62. 1854. *Panicum chrysoblephare* Steudel, Syn. Pl. Glumac. 1: 62. 1855. *Panicum chrysites* Steudel, Syn. Pl. Glumac. 1: 38. 1855. *Paspalum chrysites* (Steudel) Doell in Mart., Fl. Bras. 2(2): 117. 1877. *A. aureus* P. Beauv. sensu Chase, Proc. Biol. Soc. Wash. IV: 135. 1911. *Paspalum carinatovaginatum* Mez, Feddes Repert. Spec. Nov. Regni Veg. 15: 31. 1917. *A. chrysites* (Steudel) Kuhlm., Comiss. Linhas Telegr. Estratég. Mato Grosso Amazonas 67, Annexo 5, Bot. 11: 88. 1922. *A. minutus* Luces, Bol. Soc. Venez. Cienc. Nat. 80: 22. 1953.

Several authors have treated *A. exasperatus* as a synonym of *A. aureus* P. Beauv.; however, the description given by Palisot de Beauvois (1812) applies equally well to several taxa within *Axonopus* sect. *Cabrera* and no type specimen of *A. aureus* has been located. Furthermore, Garófalo-Spalding (1988) found that Trinius (1828) misinterpreted Kunth's (Humboldt et al., 1816) description and plates of *Paspalum aureus*, which in fact conform to the presently accepted concept of *A. chrysoblepharis*. The plant portrayed in Trinius's plates belongs to the taxon here treated as *A. exasperatus*. Subsequent authors have continued this error, and Garófalo-Spalding has proposed that the name *A. aureus* P. Beauv. be abandoned as a source of confusion. In other geographic regions *A. exasperatus* is reported from a variety of well-drained and wetland habitats, but in Chiquitanía it is narrowly restricted to seasonally humid and shallowly inundated savannas; flowering December to (*January*) February. Distribution: Central America to Brazil; Bolivia: Andean Piedmont of Santa Cruz. (630, 686, 860, 1603, 1629, 1668, 1804)

A. fissifolius (Raddi) Kuhlm., Comis. Linhas Telegr. Estratég. Mato Grosso Amazonas 67, Annexo 5, Bot. 11: 87. 1922. *Paspalum fissifolium* Raddi, Agrost. Bras. 26. 1823. *P. compressum* var. *arenarium* Bertoni, Anales Ci. Parag. Ser. 2, 2: 153. 1918. *A. stragalus* Chase, Contr. U.S. Natl. Herb. 22: 472. 80. 1922. *A. affinis* Chase, J. Wash. Acad. Sci. 28: 180. 1938. *A. ater* Chase, J. Wash. Acad. Sci. 17: 143. 1927. *A. hirsutus* G. A. Black, Adv. Front. Pl. Sci. 5: 147. 1963.

Common, in valley-side *campo* (upslope) and seasonally humid or shallowly inundated savannas, rarely in superficial soil over granitic outcrops (then usually seasonally humid). This species is very palatable (4) and resistant to trampling by cattle; unlike most palatable grasses, it increases in abundance in overgrazed savannas. This is apparently due to an ability to form dense lawnlike colonies via the vigorous production of innovations and stolons, which allow it to colonize exposed soil surfaces. Colonies flower September to (*November, December*) March; $2n = 20$; local name: *grama*. Distribution: Central America to Argentina; Bolivia: Andean Piedmont of Santa Cruz, Beni, and the Yungas. (600, 611, 614, 629, 642, 674, 684, 713, 773, 1347, 1364, 1531, 1576, 1624, **2253,** 2275, 2297)

A. herzogii (Hack.) Hitchc. Contr. U.S. Natl. Herb. 24: 431. 1927. *Panicum herzogii* Hack., Feddes Repert. Spec. Nov. Regni Veg. 7: 50. 1909.

Rare, apparently known only from the type locality at Cerro San Miserato near Santiago de Chiquitos and two localities in the adjacent Brazilian states of Mato Grosso and Rondônia. This taxon is intermediate to *A. brasiliensis* and *Axonopus* sect. *Cabrera*, of which *A. chrysoblepharis*, *A. canescens*, *A. pulcher*, and *A. exasperatus* exist in Chiquitanía; it is possibly a hybrid. (BOLIVIA. SANTA CRUZ: *Cutler 7018* US; BRAZIL. MATO GROSSO: Pimenta Bueno to Riozinho, *Kuhlmann 1722* US; Serra dos Parecis, *Rosa 841* US.)

A. leptostachyus (Flügge) Hitchc., Contr. U.S. Natl. Herb. 22: 471. 1922. *Paspalum leptostachyum* Flügge, Monogr. Pasp. 122. 1810. *A. macrostachyus* Hitchc. & Chase, Contr. U.S. Natl. Herb. 18: 301. 1917.

Rare, seasonally humid savanna; flowering in January. Distribution: northern South America to Argentina. (1685)

A. marginatus (Trin.) Chase, Contr. U.S. Natl. Herb. 17: 226. 1913. *Paspalum marginatum* Trin., Gram. Panic. 90. 1826. *P. ery-*

throchaetum Mez, Feddes Repert. Spec. Nov. Regni Veg. 15: 32. 1917. *A. longecilius* (Hack.) L. Parodi, Notas Prelim. Mus. La Plata 3: 22. 1938.

Occasional, lateritic crests in *cerrado* and gravel soils of *campo rupestre*; flowering is dependent upon fire. Distribution: Brazil and Paraguay; Bolivia: the Yungas. (1138, 1200, 1389, 2229, 2789)

A. paranaensis L. Parodi ex G. A. Black, Adv. Front. Pl. Sci. 5: 168. 1963.

Rare, seasonally humid savanna; flowering in January. Distribution: Uruguay and Argentina. (1633)

A. pulcher (Nees) Kulhm., Comiss. Linhas Telegr. Estratég. Mato Grosso Amazonas 67, Annexo 5, Bot. 11: 88. 1922. *Panicum pulchrum* Willd. ex Sprengel, Syst. Veg. 1: 272. 1825, nomen nudum. *Paspalum pulchrum* Nees, Agrost. Bras. 79. 1829. *Axonopus sprucei* (Doell) G. A. Black, Adv. Front. Pl. Sci. 5: 168. 1963.

Garófalo-Spalding (1988) treated this species as a variety of *A. canescens*. Sandy soil in *campo rupestre* (Serranía San Lorenzo); flowering in April. Distribution: Colombia, Venezuela, and Brazil. (1395, 1982)

Bambusa Schreber

B. vulgaris Schrader ex Wendl. var. **vittata** A. & C. Riviére, Bull. Soc. Natl. Acclim. France III. 5: 640. 1878. *B. vulgaris* var. *striata* (Lodd.) Gamble, Ann. Roy. Bot. Gard. (Calcutta) 7: 44. 1896.

Cultivated for ornament and construction material in Concepción and San Ignacio de Velasco; local name: *bambú*.

Bothriochloa Kuntze

Allred, K. W. & F. W. Gould. 1983. Systematics of the *Bothriochloa saccharoides* complex (Poaceae: Andropogoneae). Syst. Bot. 8(2): 168–184. de Wet, J. M. J. 1968. Biosystematics of the *Bothriochloa barbinodis* complex (Gramineae). Amer. J. Bot. 55: 1246–1250.

B. exaristata (Nash) Henrard, Blumea 4: 520. 1941. *Amphilophis exaristatus* Nash in J. K. Small, Fl. S.E. U.S. 65. 1903. *Andropogon hassleri* Hack., Bull. Herb. Boisser II. 4: 266. 1904. *A. saccharoides* var. *hassleri* Ekman, Ark. Bot. 11: 8. 1912. *B. hassleri* (Hack.) Henrard, Nederl. Dendrol. Ver. Gedenkb. Suringar 184. 1942.

Rare, valley-side *campo* (midslope); flowering in November. Distribution: southern Brazil, Paraguay, Uruguay, Argentina, and the southern United States. (1516)

Brachiaria (Trin.) Griseb.

Sendulsky, T. 1978. *Brachiaria*: taxonomy of cultivated and native species in Brazil. Hoehnea 7: 99–139. Parodi, L. R. 1969. Estudios sistematicos sobre las Gramineae–Paniceae argentinas y uruguayas. Darwiniana 15(1–2): 65–111.

KEY TO SPECIES

1a. Upper floret beaked, apex of pedicels with a ring of stout hairs ..... *B. paucispicata*
1b. Upper floret not beaked, apex of pedicels glabrous or pubescent, lacking ring of stout hairs.
  2a. Spikelets 2–3 mm long.
    3a. Glumes and lower lemma glabrous, reticulately veined between the nerves; upper floret subglobose ..... *B. lorentziana*
    3b. Glumes and lower lemma hirsute, not reticulately veined; upper floret ovate ..... *B. echinulata*
  2b. Spikelets 4–6 mm long.
    4a. Rachis about 1 mm wide ..... *B. brizantha*
    4b. Rachis about 2 mm wide.
      5a. Glumes and lower lemma sparsely pubescent, at least at apex of upper glume; rhizomatous perennial ..... *B. decumbens*
      5b. Glumes and lower lemma glabrous; duration indefinite, decumbent and rooting at the nodes ..... *B. plantaginea*

B. brizantha (Hochst. ex A. Rich.) Stapf in Prain, Fl. Trop. Africa 9: 531. 1919. *Panicum brizanthum* Hochst. ex A. Rich., Fl. Abyss. 2: 363. 1851.

A newly introduced cultivated perennial forage grass of African origin, which intergrades with *B. decumbens*; flowering January to April; local name: *bracherón*. (1704, 1963)

B. decumbens Stapf in Prain, Fl. Trop. Africa 9: 528. 1919. *Panicum eminii* Mez, Bot. Jahrb. 34: 135. 1904, non *P. eminens* Steudel, Syn. Pl. Glum. 1: 43. 1854. *B. eminii* (Mez) Robyns, Bull. Jard. Bruxelles 9: 176. 1932.

Although *P. eminii* Mez and *P. eminens* Steudel are not homonyms in the strict sense, they are sufficiently similar to be confused. Since *B. decumbens* is the traditional name for this widely cultivated forage grass, its usage is retained. This species attained wide popularity in the 1980s due to improved productivity compared with *Hyparrhenia rufa* (Patterson, 1984), but current cultivars have become susceptible to an insect pest (*salivaso*), and ranchers are diversifying their forage resources; flowering December to February. (618, 745, 1230, 1705)

B. echinulata (Mez) L. Parodi, Darwiniana 15(1–2): 94. 1969. *Panicum echinulatum* Mez, Notizbl. Bot. Gart. Berlin-Dahlem 7: 62. 1917. *P. echinulatum* var. *boliviense* Henrard, Meded. Rijks-Herb. 40: 50. 1921.

Rare, as a weed in pastures at San José de Chiquitos. Distribution: Argentina and Paraguay; Bolivia: the Yungas, Beni, and Tarija. (1699)

B. lorentziana (Mez) L. Parodi, Darwiniana 15(1–2): 99. 1969. *Panicum lorentziana* Mez, Bot. Jahrb. Syst. 56(125): 1. 1921. *P. velutinosum* Nees f. *violascens* Stuckert, Anales Mus. Nac. Hist. Nat. Buenos Aires 11: 75. 1904. *P. velutinosum* f. *viride* Stuckert, Anales Mus. Nac. Hist. Nat. Buenos Aires 11: 75. 1904.

Rare, as a weed along logging road in seasonal forest; flowering in March. Distribution: northern Argentina. (1887)

B. paucispicata (Morong) Clayton, Kew Bull. 42: 402. 1987. *Panicum paucispicatum* Morong, Ann. N.Y. Acad. Sci. 7: 262. 1893. *Acroceras paucispicatum* (Morong) Henrard, Blumea 3: 411–480. 1940.

Rare, in seasonally inundated swamps (*palmares*) dominated by *Copernicia alba* Morong, near San José de Chiquitos and the seasonally humid savannas of the Andean Piedmont; flowering in January. Distribution: Paraguay and the Gran Chaco of Argentina. (1585, 1707)

B. plantaginea (Link) Hitchc., Contr. U.S. Natl. Herb. 12: 212. 1909. *Panicum plantaginum* Link, Hort. Berol. 1: 206. 1827. *P. leandri* Trin., Sp. Gram. 3(28): 335. 1835.

Rare, as a weed of gardens. Distribution: southern United States to northern Argentina. (1810)

Cenchrus L.

DeLisle, D. G. 1963. Taxonomy and distribution of the genus *Cenchrus*. Iowa State J. Sci. 37(3): 259–351. Filgueras, T. S. 1984. O gênero *Cenchrus* no Brasil (Gramineae; Panicoideae). Acta Amazonica 14(1, 2): 95.

KEY TO SPECIES (PLUS A SUPERFICIALLY SIMILAR SPECIES OF *PENNISETUM*)

1a. Inner whorl of spines united for ½–¾ the length of bur.
  2a. Involucre a flattened inner whorl of spines and an outer whorl of free, terete bristles.
    3a. Outer bristles as long as the inner spines ..... *C. brownii*
    3b. Outer bristles much shorter than the inner spines ..... *C. echinatus*
  2b. Involucre composed of flattened spines only, which arise at irregular intervals ... *C. incertus*
1b. Inner whorl of spines or bristles connate only at base.
  4a. One bristle distinctly longer than the rest, the inner whorl finely ciliate ..... *Pennisetum ciliare*
  4b. All spines of equal length, scabrous ..... *C. myosuroides*

C. brownii Roemer & Schultes, Syst. Veg. 2: 258. 1817. *C. viridis* Sprengel, Syst. Veg. 1: 301. 1824.

Occasional as a weed in streets and yards of villages; flowering in June. Distribution: throughout the tropics. (976)

C. echinatus L., Sp. Pl. 1050. 1753. *C. pungens* H.B.K., Nov. Gen. Sp. 1: 115. 1816. *C. lechleri* Steudel in Lechl., Berberid. Amer. Austr. 56. 1857. *C. crinitus* Mez., Notizbl. Bot. Gart. Berlin-Dahlem 7: 48. 1917; see DeLisle (1963) for an extensive synonymy.

A rare weed in sandy soils of the Andean Piedmont; flowering in August. Distribution: southern United States to Argentina and the Pacific Islands; Bolivia: Andean Piedmont of Santa Cruz and the Yungas. (1118)

C. incertus M. A. Curtis, Bost. J. Nat. Hist. 1: 135. 1837. *C. pauciflorus* Benth., Bot. Voy. Sulph. 56. 1844. *C. muricatus* Philippi, Sert. Mend. Atl. 44. 1870, non L., 1771. *C. hu-*

milis Hitchc., Contr. U.S. Natl. Herb. 24: 488. 1927.

Rare, thorn scrub of the Gran Chaco. Distribution: Mexico and the West Indies to Argentina and Chile; Bolivia: Sorata and Tarija. (1281)

C. myosuroides H.B.K., Nov. Gen. Sp. 1: 115, pl. 35. 1816. *Pennisetum myosuroides* Sprengel, Syst. Veg. 1: 303. 1825. *C. alopecuroides* C. Presl, Rel. Haenk. 1: 317. 1835, non Thunb., 1794. *C. scabridum* Arechav., Anales Mus. Nac. Montevideo 1: 556. 1895.

Rare or overlooked roadside weed in sandy soils of the Gran Chaco. Distribution: southern United States to Argentina; Bolivia: Tarija and Cochabamba. (1313)

Chloris Sw.

Anderson, D. E. 1974. Taxonomy of the genus *Chloris* (Gramineae). Brigham Young Univ. Sci. Bull., Biol. Ser. 19(2): 1–133.

KEY TO SPECIES

1a. Margins of lemma long-ciliate above (hairs 2 mm long) and short-ciliate below (hairs 0.5 mm long); spikes 3–6(8) cm long ..... *C. virgata*
1b. Margins of lemma uniformly long-ciliate (hairs 1.5–2 mm long); spikes 10–20 cm long ..... *C. dandyana*

C. dandyana C. D. Adams, Phytologia 21: 408. 1971. *Andropogon barbatum* L., Syst. Nat. ed. 10. 2: 1305. 1759. *Andropogon polydactylon* L., Sp. Pl. 2: 1483. 1763. *Chloris polydactyla* (L.) Sw., Prodr. 26. 1788. *C. consanguinea* Kunth, Révis. Gramin. 1: 89. 1829. *C. elata* Desv., Opusc. Sci. Phys. Nat. 73. 1831. *C. arundinacea* Nees ex Steudel, Syn. Pl. Glumac. 1: 207. 1854. *C. barbata* (L.) Nash, Bull. Torrey Bot. Club 25: 443. 1898. *C. polydactyla* f. *stolonifera* L. Parodi, Revista Argent. Agron. 20: 24. 1953.

Occasional roadside weed; flowering October to January. Distribution: United States to Argentina. (1238, 1268, 1311, 1692)

C. virgata Sw., Fl. Ind. Occ. 1: 203. 1797. *Chloris elegans* H.B.K, Nov. Gen. Sp. 1: 166. 1816.

Roadside weed, Gran Chaco; flowering in October. Distribution: throughout the tropics. (1269)

Chusquea Kunth

Clark, L. G. 1989. Systematics of *Chusquea* section *Swallenochloa*, section *Verticillatae*, and section *Serpentes* and section *Longifoliae* (Poaceae: Bambusoideae). Syst. Bot. Monogr. 27: 1–127.

C. ramosissima Lindman, Köngl. Svenska Vetensk. Akad. Handl. 34(6): 24. 1900. *C. phacellophora* Pilger, Notizbl. Bot. Gart. Berlin-Dahlem 8: 456. 1923.

Rare, liana in seasonal forest; vigorous growth noted in forest gaps; Rancho Zapoco 60 km SE of Concepción. Distribution: Brazil and Paraguay. (1529, 1530)

Coelorachis Brongniart

Veldkampf, J. F., R. de Koning & M. S. M. Sosef. 1986. Generic delimitation of *Rottboellia* and related genera (Gramineae). Blumea 31: 281–307. Quarín, C. L. 1979. Los géneros *Rhytachne* y *Coelorachis* (Gramineae) en Argentina. Kurtziana 12–13: 7–35. Clayton, W. D. 1970. Studies in the Gramineae 21. *Coelorachis* and *Rhytachne*: a study in numerical taxonomy. Kew Bull. 24: 309–314.

C. aurita (Steudel) A. Camus., Ann. Soc. Linn. Lyon 68: 197. 1922. *Rottboellia aurita* Steudel, Syn. Pl. Glumac. 1: 361. 1854. *Manisuris aurita* (Steudel) Kuntze, Revis. Gen. Pl. 3: 356. 1898. *Mnesithea aurita* (Steudel) Koning & Sosef, Blumea 31(2): 302. 1986.

Common, valley-side *campo*, seasonally inundated savanna, savanna marsh, and seasonal ponds; palatable (3); flowering November to (*December*, *January*, *February*) June; $2n = 18$. Distribution: Central America to Argentina; Bolivia: Andean Piedmont of Santa Cruz and the Beni. (623, 624, 817, 1528, 1592, 1789, **2287**)

Cynodon L. C. Rich.

de Wet, J. M. J. & J. R. Harlan. 1970. Biosystematics of *Cynodon* L. C. Rich. (Gramineae). Taxon 19: 565–569. Caro, J. A. & E. Sánchez. 1969. Los especies de *Cynodon* (Gramineae) de la República Argentina. Kurtziana 5: 191–252.

KEY TO SPECIES

1a. Spikelets 2.0–2.5 mm long; inflorescence a digitate whorl of 3–4 spikes 3–6 cm long ..... *C. dactylon*

1b. Spikelets 2.5–3.5 mm long; inflorescence a digitate whorl of 4–8 spikes 6–10 cm long ..... *C. nlemfuensis*

C. dactylon (L.) Pers., Syn. Pl. 85. 1805. *Panicum dactylon* L., Sp. Pl. 58. 1753. *C. maritimus* H.B.K., Nov. Gen. Sp. 1: 170. 1816. *C. pascuus* Nees, Agrost. Bras. 425. 1829. *C. erectus* C. Presl, Rel. Haenk. 1: 290. 1830.

An extremely variable taxon, Caro & Sánchez (1969) described numerous species, which are better viewed as varieties of this vegetatively reproducing species. Common as a weed in pastures and along roads; palatable (5), cultivated as forage for chickens and pigs; local name: *bremura, bremura costal.* Distribution: throughout the tropics; abundant along roadsides in the Gran Chaco. (741)

C. nlemfuensis Vanderyst, Bull. Agric. Congo. Belge 13: 342. 1922. *C. dactylon* (L.) Pers. var. *sarmentosus* L. Parodi, Revista Argent. Agron. 23: 185. 1956. *C. plectostachyus* sensu Caro & Sánchez, Kurtziana 5: 213. 1969.

Cultivated forage grass, not widely planted in Chiquitanía but common in the Gran Chaco; flowering November to May; local name: *estrella africana.* (978, 1387)

Dactyloctenium Willd.

D. aegyptium (L.) Willd., Enum. Pl. 1029. 1809. *Cynosurus aegyptius* L., Sp. Pl. 72. 1753. *D. mucronatum* (Michx.) Willd., Enum. Pl. 1029. 1809.

Rare, roadside weed. Distribution: throughout the tropics. (1700)

Digitaria Haller

Henrard, J. T. 1950. Monograph of the genus *Digitaria.* Univ. Pers. Leiden. Veldkampf, J. F. 1973. A revision of *Digitaria* Haller (Gramineae) in Malesia. Blumea 21: 1–80. Rugolo de Agrasar, Z. 1974. Las especies del género *Digitaria* (Gramineae) en la Argentina. Darwiniana 19(1): 65–171. Webster, R. D. 1987. Taxonomy of *Digitaria* section *Digitaria* in North America (Poaceae, Paniceae). Sida 12(1): 209–222.

KEY TO SPECIES

1a. Spikelets villous or densely pubescent, the hairs 1.5–10 mm long (at least at base of spikelet).
  2a. Spikelet hairs 1.5 mm long (shorter at apex of glume and lower lemma); base of the plant invested with senescent sheaths of previous years' growth; innovations intravaginal; culms unbranched, 0–1 nodes visible above the basal foliage ..... *D. neesiana*
  2b. Spikelet hairs 5–10 mm long; base of plant not shrouded by senescent sheaths; foliage cauline (at least at maturity); innovations extravaginal; culms freely branched, 3–6 nodes visible above the basal foliage ..... *D. insularis*
1b. Spikelets glabrous, short-pubescent or ciliate, the hairs, when present, less than 0.5 mm long.
  3a. Upper floret dark reddish brown; spikelets borne in triads; racemes inserted on an elongate axis.
    4a. Spikelets 2–2.5 mm long, obovate; pubescence of glumes and lower lemma conspicuously and uniformly of short, glandular-tipped hairs ..... *D. mattogrossensis*
    4b. Spikelets 1–1.8 mm long, lanceolate; pubescence of glumes and lower lemma in lines between margins, not glandular.
      5a. Racemes 3–8(10); spikelets 1.5–1.8 mm long ..... *D. fragilis*
      5b. Racemes (8)10–30; spikelets 1–1.3 mm long ..... *D. lehmanniana*
  3b. Upper floret lead-colored, green, or tan; spikelets borne in pairs; racemes conjugate or digitate.
    6a. Racemes 2, conjugate; plants stoloniferous ..... *D. fuscescens*
    6b. Racemes 2–many, digitate at 1 or 2 nodes; plants of indefinite duration, decumbent and rooting at the nodes.
      7a. Lower glume lacking.
        8a. Upper glume and lower lemma glabrous; upper glume equaling upper floret ..... *D. lanuginosa*
        8b. Upper glume and lower lemma ciliate; upper glume about ½ the length of upper floret ..... *D. setigera*
      7b. Lower glume present.
        9a. Spikelets dimorphic, the pedicellate spikelet with stiffly spreading marginal hairs, the hairs lacking on sessile spikelet ..... *D. bicornis*
        9b. Spikelets all alike, the pedicellate and sessile spikelet both with ascending marginal hairs ..... *D. ciliaris*

D. bicornis (Lam.) Roemer & Schultes, Syst. Veg. 2: 470. 1817. *Paspalum bicorne* Lam., Tabl. Encycl. 1: 176. 1791. *Syntherisma sanguinalis* sensu Hitchc., Contr. U.S. Natl. Herb. 24(8): 425. 1927 (in part). *D. diversiflora* Swallen, Rhodora 65: 356. 1963.

Common, as a weed of pastures and roadsides in forest and *cerrado* soils; flowering throughout

the year. Distribution: pantropical. (1262, 1280, 1406, 1539, 1696)

D. ciliaris (Retz.) Koel., Descr. Gram. 27. 1802. *Panicum ciliare* Retz., Observ. Bot. 4: 16. 1786. *Panicum adscendens* H.B.K., Nov. Gen. Sp. 1: 80. 1816. *D. adscendens* (H.B.K.) Henrard, Blumea 1: 92. 1934. *Syntherisma sanguinalis* sensu Hitchc., Contr. U.S. Natl. Herb. 24(8): 425. 1927 (in part); see Veldkampf (1973) for extensive synonymy.

Common, as a weed of pastures and roadsides in forest and *cerrado* soils; rarely naturalized in superficial soils over granitic outcrops; flowering throughout the year. Distribution: throughout temperate and tropical regions of the New World. (603, 608, 678, 743, 1126, 1280, 1541, 1672, 1701, 2303)

D. fragilis (Steudel) Luces, J. Wash. Acad. Sci. 32: 160. 1942. *Paspalum fragile* Steudel, Syn. Pl. Glumac. 1: 19. 1854.

Common along roads in *cerrado*; occasional on superficial gravel soils of granitic outcrops and lateritic crests; flowering October to December. Distribution: Venezuela and Colombia. (638, 798, 837, 1233, 1329, 1538, 1786)

D. fuscescens (C. Presl) Henrard, Meded. Rijks-Herb. 61: 8. 1930. *Panicum fuscescens* C. Presl, Rel. Haenk. 213. 1830. *Syntherisma fuscescens* (C. Presl) Scribner, Ann. Rep. Missouri Bot. Gard. 10: 49, t. 10. 1899.

Occasional as a weed in compacted gravel soils of road embankments; flowering January to February. Distribution: throughout the tropics. (786, 1661, 1734)

D. insularis (L.) Mez ex Ekman, Ark. Bot. 11: 17. 1912. *Andropogon insularis* L., Syst. Nat. ed. 10. 2: 1304. 1759. *Panicum leucophaeum* H.B.K., Nov. Gen. Sp. 1: 97. 1816. *Acicarpa sacchariflora* Raddi, Agrost. Bras. 31, pl. I, f. 4. 1823. *Trichachne insularis* (L.) Nees, Agrost. Bras. 87. 1829. *Trichachne saccharifloruм* (Raddi) Nees, Agrost. Bras. 87. 1829. *Leptocoryphium penicilligerum* Speg., Anales Soc. Ci. Argent. 16: 102. 1883. *Valota penicilligera* (Speg.) Chase ex L. Parodi, Revista Fac. Agron. Veterin. 4: 46. 1922. *Digitaria sacchariflora* (Raddi) Henrard, Blumea 1: 99. 1934.

Abundant, an aggressive weed along roads in savanna and forest; flowering in *November, December*, and irregularly throughout the year. Distribution: southern United States to Argentina. (595, 1388, 1405, 1571, 1695, 1730)

D. lanuginosa (Nees) Henrard, Meded. Rijks-Herb. 61: 5. 1930. *Paspalum lanuginosum* Nees, Agrost. Bras. 63. 1829. *D. laetevirens* Mez, Bot. Jahrb. Syst. 56(125): 8. 1921. *Panicum cuyabense* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 3: 206. 1835. *Syntherisma cuyabensis* (Trin.) Hitchc., Contr. U.S. Natl. Herb. 22: 468. 1922. *D. cuyabensis* (Trin.) L. Parodi, Physis 8: 378. 1926.

Rare, in seasonally humid sandy soils; flowering throughout the year. Distribution: the Guianas, Brazil, Paraguay, Argentina, and Uruguay; Bolivia: Andean Piedmont of Santa Cruz. (772, 1252, 1578, 1583, 2109, 2293)

D. lehmanniana Henrard, Blumea 1: 107. 1934.

Rare, *cerrado*; flowering in November. Distribution: Colombia, Peru, and Argentina; Bolivia: the Yungas. (1488)

D. mattogrossensis (Pilger) Henrard, Meded. Rijks-Herb. 61: 1. 1930. *Panicum adustum* Nees var. *mattogrossensis* Pilger, Bot. Jahrb. Syst. 30: 131. 1901.

Rare, *cerrado*/forest margin; flowering in *March* and April. Distribution: central Brazil. (1922, 2400)

D. neesiana Henrard, Blumea 1: 99. 1934. *Trichachne velutina* Nees, Agrost. Bras. 90. 1829, non *D. velutina* Forssk. ex P. Beauv., 1812, nec *D. velutina* (DC.) Hitchc., 1927. *Panicum vestitum* Kunth, Révis. Gramin. 1: 39. 1829, non *D. vestita* Figari & DeNotaris, 1854. *Valota vestita* (Kunth) Kuhlm., Comiss. Linhas Telegr. Estratég. Mato Grosso Amazonas 67, Annexo 5, Bot. 11: 40. 1922.

Local populations of this species are composed of functionally dioecious plants: pistillate plants have spikelets with vestigial anthers and nonfunctional pollen, while staminate plants have spikelets lacking gynoecia. Common in ungrazed *cerrado*; palatable (3); flowering is dependent upon fire; $2n$ = about 60. Distribution: Colombia and Brazil. (1140, 1192, 1457, **2189,** 2787; *Thomas 5694* NY, LPB)

D. setigera Roth ex Roemer & Schultes, Syst. Veg. 2: 474. 1817. *Syntherisma digitata*

(Sw.) Hitchc., Contr. U.S. Natl. Herb. 12: 142. 1908 (in part).

Similar to *D. horizontalis* Willd., which has a vestigial lower glume. Rare but probably overlooked, a roadside weed. Distribution: throughout the tropics. (1427)

Echinochloa P. Beauv.

Gould, F. W., M. A. Ali & D. E. Fairbrothers. 1972. A revision of *Echinochloa* in the United States, Amer. Midl. Naturalist 87: 36–59.

KEY TO SPECIES

1a. Spikelets about 2 mm long, the lower lemma acute to mucronate; racemes unbranched, the spikelets crowded and regularly 4-rowed ..... *E. colona*

1b. Spikelets 2.5–3.2 mm long, the lower lemma mucronate to aristate; lower racemes branched, irregularly 4-rowed ..... *E. cruz-pavonis*

E. colona (L.) Link, Hort. Berol. 2: 209. 1833. *Panicum colonum* L., Syst. Nat. 10(2): 870. 1759. *Oplismenus colonus* (L.) H.B.K., Nov. Gen. Sp. 1: 108. 1816.

Occasional, roadside ditches. Distribution: throughout the tropics. (2299B, 2304)

E. cruz-pavonis (H.B.K.) Schultes, Mant. 2: 269. 1824. *Oplismenus cruz-pavonis* H.B.K., Nov. Gen. Sp. 1: 108. 1816. *Panicum sabulicola* Nees, Agrost. Bras. 258. 1829. *E. sabulicola* (Nees) Hitchc., Contr. U.S. Natl. Herb. 17: 257. 1913. *E. crusgalli* var. *cruz-pavonis* (H.B.K.) Hitchc., Contr. U.S. Natl. Herb. 22: 148. 1920.

Occasional, roadside ditches. Distribution: throughout the tropics. (2299, 1718)

Echinolaena Desv.

KEY TO SPECIES

1a. Lower glume cuspidate, about 5 mm long, surpassing the spikelet but not foliaceous, glabrous; racemes 3–6, ascending; caespitose perennial with stout culms ..... *E. minarum*

1b. Lower glume foliaceous, 10–15 mm long, coarsely papillose-hispid (rarely glabrous); raceme 1, reflexed; duration indefinite, the culms delicate, decumbent and rooting at the nodes ..... *E. gracilis*

E. gracilis Swallen, J. Wash. Acad. Sci. 23: 457. 1933.

Rare but inconspicuous and probably overlooked, seasonally inundated savanna; flowering December to May. Distribution: Central America, Colombia, and Venezuela; Bolivia: the Beni. (2083, 2261, 2415; *Bruderreck 289* ICS, LPB)

E. minarum (Nees) Pilger, Notizbl. Bot. Gart. Berlin-Dahlem 11: 246. 1931. *Oplismenus minarum* Nees, Agrost. Bras. 268. 1829. *Ichnanthus minarum* (Nees) Doell in Mart., Fl. Bras. 2(2): 294. 1877. *I. lilloi* Hack. ex Stuckert, Ann. Conserv. Jard. Bot. Genéve 17: 288. 1914. *I. sandiense* Mez, Bot. Jahrb. Syst. 56(124): 5. 1921. *I. riparia* Swallen, Phytologia 11: 150. 1964.

Rare, scrub thickets on margins of granitic outcrops; flowering in *February*; $2n = 20$. Distribution: Peru, Brazil, and Argentina; Bolivia: Cochabamba and the Yungas. (1820, **2333**)

Eleusine Gaertn.

E. indica (L.) Gaertn., Fruct. & Sem. 1: 8. 1788. *Cynosurus indicus* L., Sp. Pl. 72. 1753.

Common, weed of roadsides and gardens; flowering throughout the year. Distribution: throughout the tropics. (597, 742)

Elionurus Willd.

Renvoize, S. A. 1978. Studies in *Elionurus* (Gramineae). Kew Bull. 32(3): 665–672.

KEY TO SPECIES

1a. Culms slender, at most 1 mm in diameter, unbranched (rarely with a second terminal raceme); cilia of lower glume of sessile spikelet not lashlike, of varying lengths ..... *E. muticus*

1b. Culms stouter, 2–5 mm in diameter, branched to produce 3–8 terminal and axillary racemes; cilia of lower glume of sessile spikelet lashlike, longer below, gradually reduced towards apex of lower glume.

2a. Lower glume of sessile spikelet 2 mm wide, the nerves 10–13, distinct ..... *E. rostratus*

2b. Lower glume of sessile spikelet 1–1.5 mm wide, the nerves 5–7, indistinct.

3a. Back of lower glume of sessile spikelet glabrous to sparsely pilose; cilia of lower glume of sessile spikelet 0.2 mm long ..... *E. tripsacoides*

3b. Back of lower glume of sessile spikelet pubescent, cilia of lower glume of sessile spikelet 0.8 mm long ..... *E. ciliaris*

E. ciliaris H.B.K., Nov. Gen. Sp. 1: 193. 1816. *E. tripsacoides* var. *ciliaris* (H.B.K.) Hack. in A. DC., Monogr. Phan. 6: 333. 1889.

Intergrading with *E. tripsacoides* and *E. muticus*. Uncommon, as a weed of roadsides, pastures,

and disturbed *cerrado* near villages; unpalatable (0); flowering July to January, possibly stimulated by fire. Distribution: Mexico to Bolivia. (1408, 1682, 1683, 2118, 2774, 2820)

E. muticus (Spreng.) Kuntze, Révis. Gen. Pl. 3(2): 350. 1898. *Lycurus muticus* Sprengel, Syst. Veg. 4(2): 32. 1827. *Andropogon candidus* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 2: 260. 1832. *A. adustus* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 2: 259. 1832. *E. latiflorus* Nees in Steudel, Syn. Pl. Glumac. 1: 364. 1854. *E. candidus* (Trin.) Hack. in Mart., Fl. Bras. 2(3): 306. 1883. *E. adustus* (Trin.) Ekman, Ark. Bot. 13(10): 5. 1913. *E. viridulus* Hack. in Stuck., Anales Mus. Nac. Hist. Nat. Buenos Aires 13: 414. 1906.

An extremely variable taxon with numerous local races (allopatric species?). The most striking divergence in Chiquitanía can be observed in *campo rupestre* populations: on Serranía de San Lorenzo plants have villous racemes and the teeth of the lower glume of the sessile spikelet are 2–3 mm long (similar to *E. candidus* var. *bisetosus* Hack. & Lindman); in contrast, plants of the Serranía de Santiago have moderately pubescent racemes, and the teeth of the lower glume of the sessile spikelet are virtually lacking (*E. adustus*); *cerrado* populations are generally intermediate between these two extremes.

Abundant, the dominant grass in *cerrado* communities, providing more than 70% of the herbaceous cover in badly overgrazed savannas; very unpalatable (0), usually (but not always) with an odor of citrus. Cattle will only graze this species for a few weeks at the end of the dry season after it has been burned. Common but not abundant in *campo rupestre*, which is usually ungrazed; local name: *paja carona*, *paja bruta*, or *pasto amargo*; flowering is dependent upon fire; $2n = 20$. Distribution: northern South America to Argentina, tropical Africa; Bolivia: Andean Piedmont of Santa Cruz, Beni, and the Yungas. (517, 654, 734, 877, 1105, 1196, 1239, 1276, 1454, 1733, **2187,** 2777, 2785)

E. rostratus Nees, Agrost. Bras. 357. 1829. *Andropogon rostratus* (Nees) Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 2: 261. 1832.

Rare roadside weed. Distribution: Argentina; Bolivia: the Beni. (734, 770)

E. tripsacoides Humb. & Bonpl. ex Willd., Sp. Pl. 4: 941. 1806.

Restricted to the Andean Piedmont and intermontane valleys, in well-drained sandy soils; flowering in August, possibly stimulated by fire. Distribution: Mexico to Bolivia. (1113)

Eragrostis Wolf

Harvey, L. H. 1948. *Eragrostis* in North and Middle America. Ph.D. Dissertation. Univ. of Michigan, Ann Arbor, Michigan. Nicora, E. G. 1940. Nota taxonómica sobre *Eragrostis neesii* y *Eragrostis articulata*. Revista Argent. Agron. 7(4): 257–273.

KEY TO SPECIES

1a. Floret(s) 1(2–3), lemma about 1 mm long, the sterile rachilla internode prolonged past the palea; panicle 40 cm long and 20 cm wide; foliage glabrous ..... *E. airoides*
1b. Florets 2–many; lemmas, panicles, and foliage various; if only one floret developed, then the lemma greater than 1.5 mm long and the foliage pubescent.
2a. Spikelets disarticulating from the apex towards the base, the glumes persistent, the rachilla internodes and paleas falling.
3a. Panicles spicate to narrowly elliptic, the length 10 times the width; spikelets densely arranged on short, erect, or ascending branches, the lowermost distantly placed; lemmas about 1 mm long.
4a. Paleas long-ciliate on the keels; panicles spicate; plants 5–25 cm tall ..... *E. ciliaris*
4b. Paleas glabrous or minutely scabrous on the keels; panicles narrowly elliptic; plants 30–100 cm tall ..... *E. japonica*
3b. Panicles neither spicate nor narrowly elliptic, pyramidal, or ovate, the length less than 5 times the width; spikelets loosely arranged on the branches; lemmas 2–2.5 mm long.
5a. Spikelets linear, lead-colored, the length about 10 times the width; weedy annuals *E. tenuifolia*
5b. Spikelets elliptic or ovate, purple, tan, or lead-colored, the length about 3 times the width; annuals or perennials.
6a. Spikelets about 2 mm wide, the florets densely imbricate and obscuring the rachilla; annuals ..... *E. solida*
6b. Spikelets 1–1.5 mm wide, the florets loosely imbricate and the rachilla more or less visible; perennials.
7a. Spikelets tan; plants robust, the culms 1–1.5 m tall; panicles elliptic, 30–50 cm long.

8a. Panicle branches distinctly verticillate at all nodes; lemmas acute; foliage cauline ..... *E. orthoclada*
8b. Panicle branches alternate (subverticillate at the lower nodes); lemmas acuminate; foliage basal ..... *E. macrothyrsa*
7b. Spikelets lead-colored, the culms 30–70 cm tall; panicles ovoid to pyramidal, 20–30 cm long.
9a. Spikelets (1)2–4-flowered; panicle disarticulating at the base of the peduncle; culms with no nodes visible above the basal foliage ..... *E. polytricha*
9b. Spikelets 3–6-flowered; panicle not disarticulating at the base of the peduncle; culms with 1–2 nodes visible above the basal foliage ..... *E. lugens*
2b. Spikelets disarticulating from the base towards the apex, the glumes and lemmas deciduous, the rachilla and paleas persistent.
10a. Pedicels with a glandular ring (rarely lacking in *E. neesii*); foliage coarsely hirsute with papillose-based hairs; annuals; spikelets tan.
11a. Foliage cauline; culms branched at lower and middle nodes, about 60 cm tall; spikelets 2–3 mm wide, the lemmas 2.4 mm long ..... *E. chiquitaniensis*
11b. Foliage basal; culms unbranched, 10 20 cm tall; spikelets less than 2 mm wide, the lemmas 1.5 mm long.
12a. Leaf blades with glandular pits on the midnerve; panicle open ..... *E. articulata*
12b. Leaf blades lacking glandular pits; panicle contracted ..... *E. neesii*
10b. Pedicels not glandular-ringed; foliage glabrous or pubescent; annuals or perennials; spikelets purple, tan, or lead-colored.
13a. Panicle branches 0.5–2 cm long, reflexed or spreading; foliage pubescent.
14a. Leaf blades 2–10 cm long, spikelets tan, ovate-elliptic; annuals ..... *E. neesii* var. *lindmanii*
14b. Leaf blades 15–50 cm long, spikelets lead-colored, falcate at maturity; perennial bunch grasses ..... *E. perennis*
13b. Panicle branches either longer than 2 cm or ascending; foliage generally glabrous.
15a. Lower glume narrowly lanceolate, acuminate, subequaling or surpassing the adjacent floret; annuals.
16a. Axils of panicle branches and pedicels densely pilose; lemmas acuminate to cuspidate ..... *E. maypurensis*
16b. Axils of panicle branches and pedicels glabrous; lemmas acute ..... *E. rufescens*
15b. Lower glume ovate to lanceolate, only half as long as the adjacent floret; annuals or perennials.
17a. Spikelets 0.8 mm wide, the florets loosely imbricate and erect; margins of lemmas membranous; annuals ..... *E. pilosa*
17b. Spikelets 1.2–2.5 mm wide, the florets closely imbricate and spreading (or ascending); margins of lemmas firm; perennials.
18a. Axils of panicle branches glabrous, the branches laxly ascending, 5–15 cm long; spikelets distinctly pedicellate and distantly placed, lead-colored, 1–2 mm wide; lemmas acute to blunt ..... *E. bahiensis*
18b. Axils of panicle branches pilose, the branches strictly ascending, 1–5 cm long; spikelets subsessile, crowded, tan with purple spots, 2–3 mm wide; lemmas acuminate ..... *E. secundiflora*

E. airoides Nees, Agrost. Bras. 509. 1829. *Aira brasiliensis* Raddi, Agrost. Bras. 36. 1823, non *E. brasiliensis* (Raddi) Nees, 1829. *Sporobolus brasiliensis* (Raddi) Hack. ex Stuck., Anales Mus. Nac. Hist. Nat. Buenos Aires 21: 91. 1911. *Agrosticula brasiliensis* (Raddi) Herter, Revista Sudamer. Bot. 6: 145. 1940.

Uncommon, forming distinct colonies in seasonally humid and shallowly inundated savanna; flowering in January and February. Distribution: northern South America to Argentina and Uruguay. (722, 1564, 1833, 2321)

E. articulata (Schrank) Nees, Agrost. Bras. 502. 1829. *Poa articulata* Schrank, Sylloge Ratisb. 1: 194. 1827. *E. glareosa* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 1: 406. 1831. *E. articulata* var. *glabrescens* Henrard, Meded. Rijks-Herb. 40: 69. 1921. *E. neesii* var. *laxa* Jedwabn., Bot. Arch. 5: 206. 1924. *E. articulata* var. *eglandulosa* Nicora, Revista Argent. Agron. 7: 259, 272, f. 4, 3. 1940.

As treated by Nicora (1940), the *E. articulata* complex is composed of two species with several intergrading varieties, all of which are small caespitose annuals with basal, coarsely hirsute foliage. Some Bolivian specimens are intermediate between the varietal taxa (Table 4). Common, superficial soils over granitic outcrops and lateritic crests; occasional, as a weed along roads and as a pioneer of sand dunes in the Andean Piedmont; flowering

TABLE 4. Morphological variation for selected characters in the *Eragrostis articulata* complex.

	Glandular midnerve[1]	Contracted panicle	Glandular pedicel	Sulcate caryopsis	Basal foliage	Branched culms
E. neesii	−	+	+	−	+	−
var. *expansiflora*	−	−	+	−	+	−
var. *lindmanii*	−	+	−	−	+	−
Killeen 1338[2]	−	+/−	−	+	+	−
E. articulata	+	−	+	+	+	−
Killeen 1247[2]	+	−	+	−	+	−
var. *eglandulosa*	−	+/−	+	+	+	−
E. chiquitaniensis	+	−	+	−	−	+

[1] Refers to the midnerve of the leaf blade.
[2] Intermediate specimens provisionally placed in the preceding taxon.

August to January? Distribution: Brazil, Paraguay, and Argentina; Bolivia: Cochabamba, Andean Piedmont of Santa Cruz, and the Gran Chaco. (1122, 1247, 1481, 1568)

E. bahiensis Schrader ex Schultes, Mant. 2: 318. 1824. *Poa microstachya* Link, Hort. Berol. 1: 185. 1827. *E. expansa* Link, Hort. Berol. 1: 190. 1827. *E. psammodes* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 1: 400. 1831. *E. firma* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 4(1): 74. 1838. *E. blepharophylla* Jedwabn., Bot. Arch. 5: 197. 1924. *E. macra* Jedwabn., Bot. Arch. 5: 200. 1924.

A difficult taxon with variable inflorescence morphology and indeterminate spikelets (i.e., the number of florets/spikelet ranges from 5 to 30 depending upon the robustness of the individual plant). Occasional, valley-side *campo* (upslope), seasonally humid savanna, and seasonal ponds; frequently in disturbed habitats; flowering throughout the year; $2n = 60$. Distribution: Peru, Brazil, Paraguay, and Argentina: apparently introduced into the United States; Bolivia: Andean Piedmont of Santa Cruz and the Yungas. (779, 782, 785, 821, 1125, 1235, 1256, 1336, 1579, 1656, 1664, 1809, 2110, **2271**; *Bruderreck 108* ISC, LPB)

E. chiquitaniensis Killeen, sp. nov. TYPE: Bolivia. Santa Cruz: Estancia San Ignacio, 25 km N of San José de Chiquitos, Prva. Chiquitos, 17°35′S, 60°45′W, 320 m, 1 Feb. 1986, *Killeen 1728* (holotype, ISC; isotypes, LPB, F, MO, US, SI, NY, CTE). Figure 3.

E. articulata (Schrank) Nees affinis sed robustis, 60 cm altis, culmis 4–6-nodis, ramificantibus copiose ad nodos medios et infernos; foliis caulinis, laminis 15–25 cm longis, 4–7 mm latis; paniculis 16–27 cm longis, 4–6 cm latis; spiculis 2–4 mm latis, lemmatibus 2.0–2.5 mm longis notabilis.

Caespitose annuals; culms branched, 60 cm tall, glabrous. Foliage cauline, coarsely hirsute with papillose-based hairs; sheaths longer than the internodes below but shorter than internodes at upper nodes, glandular-pitted on the abaxial midrib; ligules ciliate, 1 mm long; blades cordate based, flat, lax, 15–25 cm long, 4–7 mm wide, broadest at the base, the apex long acuminate. Inflorescence an open, elliptic panicle, 16–27 cm long and 4–6 cm wide; branches alternate to subverticillate at the lower nodes, ascending; axils of branches glandular, bearded with stiffly spreading hairs; axis, branches, and pedicels scabrous; pedicels 2–10 mm long, ascending, with a glandular ring 1–2 mm below the insertion of the spikelet. Spikelets pyramidal, 4–12-flowered, the lower bracts spreading, the upper ascending, 4–8 mm long, 2–4 mm wide, glabrous; disarticulation from the base of the spikelet towards the apex, the glumes and lemmas falling, the rachilla and paleas persistent; lower glume ovate, acute, 1.4–1.8 mm long, keeled, the lateral nerves indistinct; upper glume similar, 1.6–2.2 mm long, covering ½ of the adjacent lemma; lemmas ovate, acute, keeled at the apex, rounded at the base, the lateral nerves indistinct but visible, 2.4 mm long, 0.4 mm wide when folded; palea 1.6 mm long, minutely ciliate on the keels; caryopsis 0.6 × 0.6 mm, truncate, not sulcate.

This species is closely related to *E. articulata* but differs by its more robust habit, branched culm, cauline foliage, and larger spikelets. Locally common in an open deciduous savanna woodland with a canopy 10–15 m tall and about 60% grass cover. The land north of San José de Chiquitos has relatively fertile, alluvial soils and is rapidly being converted to mechanized agriculture; if narrowly

FIGURE 3. *Eragrostis chiquitaniensis* (*Killeen 1728*).—A. Habit and inflorescence (bar = 5 cm).—B. Spikelet and pedicel (bar = 1 mm; arrow pointing to glandular ring on pedicel).

restricted to this area, this species will soon be extinct.

E. ciliaris (L.) R. Br. in Tuckey, Narr. Exp. Congo 478. 1818. *Poa ciliaris* L., Syst. Nat., ed. 10. 8: 875. 1759. *Macroblepharus contractus* Philippi, Linnaea 19: 101. 1858.

Common as a weed in streets, yards, and gardens of villages. Distribution: throughout the tropics. (795)

E. japonica (Thunb.) Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 1: 405. 1831. *Poa japonica* Thunb., Fl. Japon. 51. 1784. *P. glomerata* Walter, Fl. Carol. 80. 1788. *E. hapalantha* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 1: 409. 1831. *E. interrupta* (Lam.) Doell in Mart., Fl. Bras. 2(3): 157. 1878. *E. glomerata* (Walter) L. Dewey, Contr. U.S. Natl. Herb. 2: 543. 1894.

Not yet collected in Chiquitanía, as a weed in sandy soils along roads on the Andean Piedmont of Santa Cruz. Distribution: throughout the tropics. (2731)

E. lugens Nees, Agrost. Bras. 505. 1829. *E. flaccida* Lindman, Köngl. Svenska Vetensk. Acad. Handl. 34(6): 17. 1900.

Similar to *E. soratensis* Jedwabn., which has 3–6 florets but narrower panicles and no visible nodes above the foliage. Rare in Chiquitanía, more common in the Gran Chaco and Andean Piedmont; flowering is stimulated by fire, October to January. Distribution: southern United States to Argentina; Bolivia: Tarija and the Andean Piedmont of Santa Cruz. (1237, 1277, 1565, 1573)

E. macrothyrsa Hack., Feddes Repert. Spec. Nov. Regni Veg. 8: 47. 1910.

Rare, a single population 10 km S of Concepción, *cerrado*/forest margin; flowering in March. Distribution: Argentina and Paraguay. (1832)

E. maypurensis (H.B.K.) Steudel, Syn. Pl. Glumac. 1: 276. 1854. *Poa maypurensis* H.B.K., Nov. Gen. Sp. 1: 161. 1816. *P. racemosa* Vahl, Ecolg. Amer. 1: 7. 1796, non Thunb., 1794. *P. vahlii* Roemer & Schultes, Syst. Veg. 2: 563. 1817. *E. vahlii* (Roemer & Schultes) Nees, Agrost. Bras. 499. 1829. *E. acuminata* Doell in Mart., Fl. Bras. 2(3): 153. 1878.

Not yet collected in Chiquitanía but common on the Andean Piedmont of Santa Cruz and the Beni. Distribution: Mexico to Brazil.

E. neesii Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 1: 405. 1831. *E. brasiliana* Nees, Agrost. Bras. 510. 1829. *E. villosa* Steudel, Syn. Pl. Glumac. 276. 1854. *E. lindmanii* Hack., Köngl. Svenska Vetensk. Acad. Handl. 34(6): 19. 1900. *E. neesii* var. *lindmanii* (Hack.) Ekman, Ark. Bot. 13(10): 51. 1913.

Specimens without glandular pedicels are usually placed in *E. neesii* var. *lindmanii* (Table 4). Occasional, superficial soils over granitic outcrops and lateritic crests in *cerrado*; flowering October to February. Distribution: Brazil, Paraguay, Uruguay, and Argentina. (pedicels glandular: 592, 805; lacking glands on pedicels: 747, 1338, 1800)

E. orthoclada Hack., Bull. Herb. Boissier II. 4(3): 281. 1904. *E. longipila* Hack. in Stuck., Anales Mus. Nac. Hist. Nat. Buenos Aires 21: 132. 1911.

Scrub forest, San José de Chiquitos; flowering in January. Distribution: Paraguay and Argentina. (1709)

E. perennis Doell in Mart., Fl. Bras. 2(3): 144. 1878.

Locally common in *cerrado* at Santiago de Chiquitos; flowering is dependent upon fire. Distribution: Brazil. (2793)

E. pilosa (L.) P. Beauv., Ess. Agrostogr. 71, 162. 1812. *Poa pilosa* L., Sp. Pl. 68. 1753.

Common, as a weed in streets and gardens of villages. Distribution: throughout the tropics. (1128)

E. polytricha Nees, Agrost. Bras. 507. 1829. *E. lugens* var. *glabrata* Doell in Mart., Fl. Bras. 2(3): 140. 1878. *E. lugens* var. *glabrescens* Doell in Mart., Fl. Bras. 2(3): 141. 1878.

Common and widespread but never abundant, *cerrado*. The panicle disarticulates at the base of the peduncle and forms a tumbleweed at maturity; flowering is dependent upon fire; $2n = 60$. Distribution: Central America to Argentina and Chile; Bolivia: Andean Piedmont of Santa Cruz. (524, 615, 1104, 1195, 1371, 2188, **2241**)

E. rufescens Schrader ex Schultes, Mant. 2: 319. 1824. *E. acicularis* Trin., Mém. Acad. Imp.

Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 1: 406. 1831. *E. multipes* S. L. Moore, Trans. Linn. Soc. Bot. II. 4: 511. 1895. *E. polyneura* Jedwabn., Bot. Arch. 5: 205. 1924.

Common, as a weed along roads in sandy or clay soils; naturalized in *cerrado* and seasonally humid savannas; flowering December to May. Distribution: Brazil. (620, 633, 780, 913, 997, 1638, 1678, 1879)

E. secundiflora C. Presl, Rel. Haenk. 1: 276. 1830. *E. compacta* Salzm. ex Steudel, Syn. Pl. Glumac. 1: 275. 1854.

Common, as a weed along paths in seasonally humid savannas and valley-side *campos*; occasional, in *cerrado*; flowering October to June. Distribution: Brazil. (613, 1337, 1342, 1358, 1482, 1542, 1665, 2457)

E. solida Nees, Agrost. Bras. 501. 1829. *E. affinis* Salzm. ex Steudel, Syn. Pl. Glumac. 1: 277. 1854.

Occasional, as a weed in *cerrado* and well-drained soils; flowering August to April. Distribution: Brazil and Paraguay. (1127, 1560, 2005; *Bruderreck 298* ISC, LPB)

E. tenuifolia (A. Rich.) Hochst. ex Steudel, Syn. Pl. Glumac. 1: 268. 1854. *Poa tenuifolia* A. Rich., Tent. Fl. Abyss. 2: 425. 1851.

Common weed along streets and yards of towns. Distribution: throughout the tropics. (598)

Eriochloa H.B.K.

Shaw, R. B. & F. E. Smiens. 1981. Anatomical and morphological characteristics of the *Eriochloa* (Poaceae) of North America. Bot. Gaz. (Crawfordsville) 142: 534–544.

KEY TO SPECIES

1a. Upper lemma with a mucro 1 mm long (hidden by the lower lemma and upper glume); panicle with 4–15 racemes; spikelets loosely arranged; rachis pubescent ..... *E. punctata*
1b. Upper lemma lacking a mucro; panicle of 1–4 racemes; spikelets regularly 2-rowed, secund; rachis densely hispid.
2a. Spikelets 3–4 mm long, culms 25–50 cm tall ..... *E. distachya*
2b. Spikelets 5–7 mm long; culms 50 100 cm tall ..... *E. grandiflora*

E. distachya H.B.K., Nov. Gen. Sp. 1: 95, t. 30. 1816. *Helopus brachystachys* Trin., Sp. Gram. 324: 277. 1831.

Common to locally abundant in savanna wetland communities; rarely in *cerrado* and superficial soils of granitic outcrops; palatable (2); flowering January to (*March*) June; $2n = 18$. Distribution: Central America to Brazil and Paraguay; Bolivia: Andean Piedmont of Santa Cruz and the Beni. (700, 895, 946, 1458, 1859, 1999, **2441**, 2592)

E. grandiflora (Trin.) Benth., J. Linn. Soc. Bot. 19: 39. 1881. *Helopus grandiflora* Trin., Sp. Gram. 3(24): 278. 1831.

Uncommon, *cerrado* and *cerrado*/forest transition; palatable (3); flowering in March and April. Distribution: Brazil and Paraguay. (1844, 1955, 2006)

E. punctata (L.) Desv. in Hamilt., Prodr. Pl. Ind. Occ. 5. 1825. *Milium punctata* L., Amoent. Acad. 5: 392. 1759. *Helopus cognatus* Steudel, Syn Pl. Glumac. 1: 101. 1854.

Common, a weed of pastures and roadside ditches; locally abundant in some seasonally inundated savannas; flowering throughout the year. Distribution: southern United States to Argentina; Bolivia: Andean Piedmont of Santa Cruz, Beni, and the Yungas. (921, 971, 996, 1187, 1316, 1506, 1714)

Eriochrysis P. Beauv.

Swallen, J. 1966. Notes on grasses. Phytologia 14(2): 88–91.

KEY TO SPECIES

1a. Leaf blades velutinous; lower glume long-ciliate, the hairs 1.5–4 mm long, very dark reddish brown, obscuring the spikelets.
2a. Hairs borne on the upper ⅛ th of the lower glume and obscuring the tridentate or blunt apex ..... *E. cayanensis*
2b. Hairs marginal only, not on the upper ⅛ th of the lower glume, the apex rounded ..... *E. ×concepcionensis*
1b. Leaf blades glabrous, scabrous, or pubescent near the junction of the sheath and blade, not velutinous; lower glume short-ciliate to subglabrous, the hairs up to 1.5 mm long (callus hairs to 3 mm), light golden-brown to whitish, not obscuring the spikelets.
3a. Lower glume obovate, rounded at apex ..... *E. laxa*
3b. Lower glume lanceolate or asymmetrically falcate, acuminate or bidentate at the apex.
4a. Panicle 6–10(15) cm long; plants 0.3–1 m tall ..... *E. holcoides*
4b. Panicle 20–30 cm long; plants 1–2 m tall ..... *E. warmingeana*

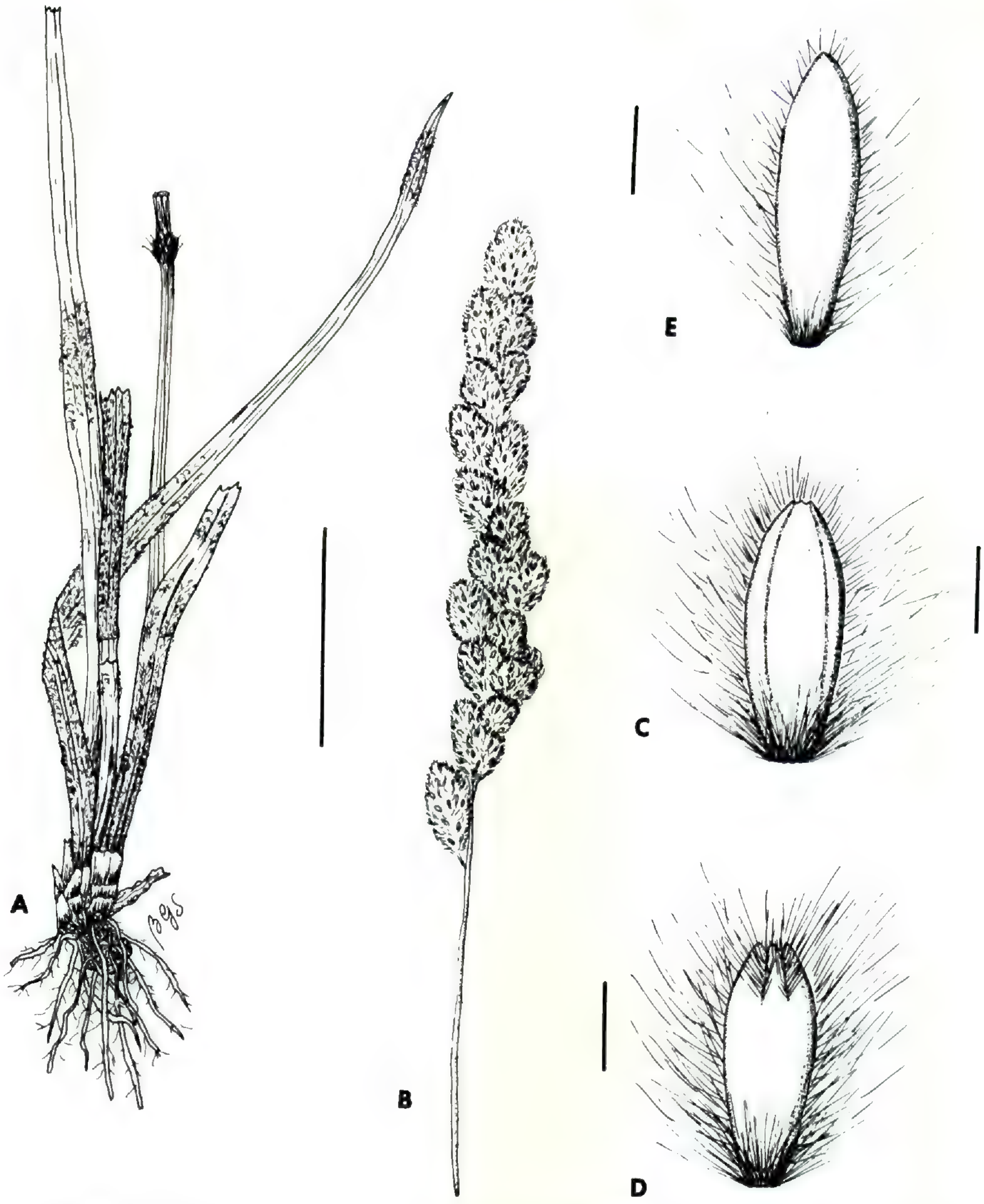

FIGURE 4. Species of *Eriochrysis*. A–C. *E.* ×*concepcionensis* (*Killeen 2384*).—A. Habit.—B. Inflorescence (A and B: bar = 5 cm).—C. Lower glume of the sessile spikelet.—D. *E. cayanensis* (*Killeen 2265*). Lower glume of the sessile spikelet.—E. *E. laxa* (*Killeen 2264*). Lower glume of the sessile spikelet (C, D, and E: bar = 1 mm).

E. cayanensis P. Beauv., Ess. Agrostogr. 8, pl. 4, f. 11. 1812. *Saccharum cayennense* (P. Beauv.) Benth., J. Linn. Soc., Bot. 19: 66. 1881.

Common, valley-side *campo* (midslope) and savanna marsh; occasional, seasonally humid or inundated savanna; rarely in seasonal ponds and laguna margins; unpalatable (0); flowering *November to January* and irregularly throughout the year; $2n = 20$. Distribution: Mexico and the West Indies to Argentina; Bolivia: Andean Piedmont of Santa Cruz and the Beni. (1131, 1346, 1438, 1510, 1594, 1860, **2265**)

E. ×concepcionensis Killeen, nothosp. nov. TYPE: Bolivia. Santa Cruz: Estancia Santa Maria, 10 km S of Concepción, Prva. Ñuflo de Chavez, 16°13′S, 62°00′W, 500 m, 16 Mar. 1987, *Killeen 2384* (holotype, ISC; isotypes, LPB, F, MO, US, SI, CTE, NY). Figure 4.

E. laxa Swallen affinis sed pilis nodis culmorum 2 mm longis; velutinis in superficiebus ambabus laminis; marginalibus glumarum ciliatis dense, pilis 1.5–3.0 mm longis, cuprinis, cum pilis callorum spiculas oscurentis notabilis.

Formula: *E. cayanensis* P. Beauv. × *E. laxa* Swallen.

Caespitose perennial; culms unbranched, the nodes densely bearded with hairs about 2 mm long, the internodes glabrous. Foliage mainly basal; sheaths glabrous below, pubescent towards the apex;

ligule a ciliate membrane 0.8 mm long; blades 6–25 cm long and 3–6 mm wide, long-attenuate at the base, reduced at upper nodes, velutinous on both surfaces, flat or involute when stressed. Inflorescence exserted, a lobed, spicate panicle 14 cm long and 1.5 cm wide, the lower branches distantly placed. Spikelets paired, sessile and pedicellate, the two spikelets bisexual and similar, occasionally only pistillate; both subtended by a bearded callus of reddish hairs 2–3 mm long; sessile spikelets 3–3.5 mm long, the pedicellate spikelets 2–2.5 mm long, largest at the base of the branches, gradually reduced in size at upper rachis nodes; disarticulation below the glumes, the sessile spikelet falling with the attached rachis internode and pedicel, the pedicellate spikelet falling separately. Lower glume narrowly elliptic to obovate, dorsally compressed, indurate and nerveless, rounded at the tip, glabrous on back, ciliate on the margins, the stiffly spreading, reddish brown hairs 1.5–3.0 mm long; upper glume laterally compressed, ciliate on the margins; lower lemma hyaline, similar to lower glume in form and length; upper lemma 1.2–1.7 mm long, hyaline, ciliate on the margins; palea minute or lacking; stamens 3, the anthers 1.5 mm long, purple-orange; lodicules membranous, strongly nerved.

A single elliptic population composed of about 300 plants growing in the same habitat with both parental species. The hybrid has the foliage vestiture and spikelet pubescence of the local forms of *E. cayanensis*, and the inflorescence morphology and the shape of the lower glume is like *E. laxa*. The three taxa were distinct and no intermediates were observed. Pollen development and seed set in the hybrid was abnormal (nonstained pollen: 82%; seed set: 0%) compared with both parents (nonstained pollen: 8% in *E. laxa* and 8% in *E. cayanensis*; seed set: 34% in *E. laxa* and 37% in *E. cayanensis*). Phenology of the hybrid is unique—the plants bloomed in *March* and April, two to three months after the peak flowering season of both parents; locally common, midslope on a valley-side *campo*. (Paratype: *Killeen 1867*)

E. holcoides (Nees) Kuhlm., Comiss. Linhas Teleg. Estratég. Mato Grosso Amazonas 67, Annexo 5, Bot. 11: 89. 1922. *Anatherum holcoides* Nees., Agrost. Bras. 324. 1829. *Andropogon holcoides* (Nees) Kunth, Révis. Gramin. 2: 49. 1829. *Saccharum holcoides* (Nees) Hack. in Mart., Fl. Bras. 2(3): 254. 1883. *S. holcoides* var. *brevipilum* Hack. in A. DC., Monogr. Phan. 126. 1889. *S. holcoides* var. *penicillare* Hack. in A. DC., Monogr. Phan. 126. 1889.

A morphologically diverse taxon; plants with burned foliage generally have asymmetrically falcate spikelets with strongly nerved, bidentate, lower glumes (*E. holcoides* s.s.); specimens with unburned foliage have elliptic to lanceolate spikelets with weakly nerved, acuminate lower glumes (*S. holcoides* var. *brevipilum* Hack.). Spikelet hairs range from almost white to dark brown (*S. holcoides* var. *penicillae* Hack.), and glumes range from glabrous to sparsely ciliate. Bolivian material collected to date is like the type of the species. Rare, valley-side *campos* (midslope); locally abundant in a boglike seep in a *campo rupestre* complex (Serranía de Santiago); flowering is dependent upon fire. Distribution: Colombia, Brazil and Paraguay. (1190, 2170, 2792)

E. laxa Swallen, Phytologia 14: 89. 1966.

Occasional, valley-side *campos* with *E. cayanensis* and *Paspalum malmeanum*; unpalatable (0); flowering October (*December*) to April; $2n = 20$. Distribution: central Brazil. (644, 737, 1365, 1437, 1595, 1870, **2264**)

E. warmingeana (Hack.) Kuhlm., Comiss. Linhas Teleg. Estratég. Mato Grosso Amazonas 67, Annexo 5, 11: 29. 1922. *Saccharum warmingiana* Hack. in Mart., Fl. Bras. 2(3): 254. 1883.

Not yet collected in Chiquitanía but probably existing in the extensive *pantanal* region of Alto Paraguá (Prva. Velasco). Distribution: Brazil; Bolivia: Andean Piedmont of Santa Cruz and the Beni where it is a zonal dominant of seasonally inundated savannas. (2596; *Steinbach 7032* US)

Eustachys Desv.

KEY TO SPECIES

1a. Lemmas lanceolate, with lashlike cilia about 10 mm long, the keel lacking or weakly developed, glabrous; racemes many ..... *E. distichophylla*

1b. Lemmas ovate, with irregular cilia 0.2–0.5 mm long, the keel strongly developed, pubescent (rarely glabrous); racemes 2–many ..... *E. caribaea*

E. caribaea (Spreng.) Herter, Rev. Sudamer. Bot. 6: 147. 1940. *Chloris caribaea* Spreng., Syst. Veg. 1: 295. 1825. *C. bahiensis* Steudel, Syn. Pl. Glumac. 1: 208. 1854. *E. bahiensis* (Steudel) Herter, Fl. Ilustr. Uruguay 1: 85, f. 339. 1941. *C. capensis* var. *bahiensis* (Steudel) L. Parodi, Revista Argent. Agron. 20: 26. 1953.

Rare, roadside weed; flowering November to February. Distribution: Brazil, Paraguay, Uruguay, and Argentina. (1407, 1713)

E. distichophylla (Lag.) Nees, Agrost. Bras. 418. 1829. *Chloris distichophylla* Lag., Gen. Sp. Pl. 4. 1816. *C. confertiflora* Trin. in Sprengel, Neue Entd. 2: 74. 1821. *C. fasciculata* Schrader ex Schultes, Mant. 2: 339. 1824. *Paspalum superbum* Sprengel, Syst. Veg. 1: 248. 1825. *C. acuminata* Trin., Sp. Gram. 3: t. 305. 1831.

Occasional, roadside weed; flowering January to June. Distribution: Peru, Brazil, Paraguay, Argentina, and Chile. (695, 977)

Gouinia Fourn.

Swallen, J. R. 1935. The grass genus *Gouinia*. Amer. J. Bot. 22: 31–41.

KEY TO SPECIES

1a. Panicle branches lacking spikelets on basal ⅓–½; lemma ciliate on the marginal nerves for ⅔–¾ of its length, the awns 2–5 mm long; culms (2)3–5 mm in diameter ..... *G. latifolia*
1b. Panicle branches bearing spikelets to the base; lemma ciliate on the marginal nerves for ⅓–½ of its length, the awns 8–15 mm long; culms 1–2 mm in diameter ..... *G. virgata*

G. latifolia (Griseb.) Vasey, Contr. U.S. Natl. Herb. 1: 365. 1895. *Tricuspis latifolia* Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 259. 1874.

Rare, roadside weed in forest; flowering in May. Distribution: Mexico to Argentina. (948)

G. virgata (C. Presl) Scribn., Bull. U.S.D.A. Div. Agrost. 4: 10. 1897. *Bromus virgatus* C. Presl, Rel. Haenk. 1: 263. 1830.

Common, roadside weed in forest soils; flowering February to June. Distribution: Mexico to Brazil. (833, 969, 1885; Puerto Suarez, *Chase 11151* US)

Guadua Kunth

Young, S. M. 1985. The taxonomy and natural history of the *Bambusa guadua* complex (Poaceae: Bambusoideae). M.S. Thesis, Univ. of Florida, Gainesville, Florida. McClure, F. A. 1973. Genera of the bamboos native to the New World (Gramineae; Bambusoideae). Smithson. Contr. Bot. 9: 1–148. 1973.

KEY TO SPECIES

1a. Culms 1–5 cm in diameter, 2–15 m tall; sheaths of culm leaves 10–30 cm long.
2a. Culms thin-walled, glabrous when young, green; pseudopetioles 10 mm long; foliage leaf blades about 7 times as long as wide ..... *G. weberbaueri*
2b. Culms solid or thick-walled, the internodes hispid, bearing irritating, whitish hairs when young, becoming glabrous with maturity, yellow-green; pseudopetioles 1–3 mm long; foliage leaf blades 10–15 times as long as wide ..... *G. paniculata*
1b. Culms 5–20 cm in diameter, 20–30 m tall; sheaths of culm leaves 30–40 cm long.
3a. Abaxial surface of sheath densely covered with irritating reddish hairs; foliage leaf blades about 30 times as long as wide; rhizomes short, the culms densely packed in clumps 3–8 m in diameter ..... *G. superba*
3b. Abaxial surface of sheath glabrous; foliage leaf blades about 10 times as long as wide; rhizomes elongate, not forming dense, well-defined clumps ..... *G. paraguayana*

G. paniculata Munro, Monogr. Bamb. 85. 1868. *Bambusa paniculata* (Munro) Hack., Oesterr. Bot. Z. 53: 195. 1903. *B. munroi* Hack., Feddes Repert. Spec. Nov. Regni Veg. 7: 374. 1909.

Abundant, forming colonies along *cerrado*/forest margins and dominating tens of thousands of hectares of low forest known locally as "*guapasales.*" Scattered populations began to flower in October 1987 after a severe drought and widespread forest floor fires; only unburned individuals were blooming initially. Populations also flowered in May 1977. Culms provide the matrix for the traditional mud and tile roof of local construction and are used to make pig-proof fences for vegetable gardens; palatable (3); local name: *guapa*. Distribution: Costa Rica to Brazil. (752, 2305, 2329, 2762, 2807; *Krapovickas & Schinini 32436* US; *Thomas 5659* NY, LPB)

G. paraguayana Doell in Mart., Fl. Bras. 2(3): 179. 1880. *Bambusa paraguayana* (Doell) Bertoni, Anales Ci. Parag. 2(2): 159. 1918.

Rare, Parque Nacional "Noel Kempff Mercado"; forming large diffuse colonies in mesic forest; local name: *taquarembó*. Distribution: Brazil, Paraguay, and northeastern Argentina. (2763, 2764)

G. superba Huber, Bol. Mus. Goeldi 4: 479. 1904. *Bambusa superba* (Huber) McClure, Smithson. Contr. Bot. 9: 68. 1973.

Locally abundant along the Río Quizer near San Ramón and 10 km northwest of San Javier; local name: *taquarembó*. Distribution: Brazil. (2302)

G. weberbaueri Pilger, Feddes Repert. Spec. Nov. Regni Veg. 1: 257. 1830. *Bambusa weberbaueri* (Pilger) McClure, Smithson. Contr. Bot. 9: 68. 1973.

A single known colony in Chiquitanía, on the grounds of the municipal swimming pool at San José de Chiquitos; local name: *taquara*. Distribution: Peru; Bolivia: the Yungas. (2818, 2627)

Gymnopogon P. Beauv.

Smith, Jr., J. P. 1971. Taxonomic revision of the genus *Gymnopogon* (Gramineae). Iowa State Univ. J. Sci. 45: 319–385.

KEY TO SPECIES

1a. Leaf blades 5 20 mm wide; awns straight, not hygroscopic; spikelets distantly placed on the lower ⅔ of the spicate branches, crowded towards apex ..... *G. spicatus*
1b. Leaf blades 3–5 mm wide; awns flexuous, hygroscopic; spikelets uniformly distributed along the whole length of the spicate branches ..... *G. fastigiatus*

G. fastigiatus Nees, Agrost. Bras. 430. 1829. *Monochaete fastigiata* (Nees) Doell in Mart., Fl. Bras. 2(3): 79. 1878. *Doellochloa fastigiata* (Nees) Kuntze, Rev. Gen. Pl. 2: 773. 1891. *G. jubiflorus* Hitchc., Contr. U.S. Natl. Herb. 24: 412. 1927. *G. fastigiatus* subsp. *jubiflorus* (Hitchc.) J. P. Smith, Iowa State Univ. J. Sci. 45: 361. 1971.

Common in valley-side *campos* (midslope), occasionally in seasonally inundated savannas and savanna marsh; flowering April to (*May*) July. Distribution: Colombia, Venezuela, and Brazil; Bolivia: Beni and the Yungas. (1029, 1144, 1350, 2039, 2077, 2588)

G. spicatus (Sprengel) Kuntze, Revis. Gen. Pl. 3(3): 354. 1891. *Polypogon spicatus* Sprengel, Syst. Veg. 1: 243. 1825. *G. biflorus* Pilger, Bot Jahrb. Syst. 30: 139. 1901.

Plants are variable within populations for stature, size of inflorescence, and the number of florets/spikelet. This species is a common constituent of *cerrado*, occupying open spaces between large bunch grasses; unpalatable (0); flowering February to (*May*) July; $2n = 20$. Distribution: Mexico to Uruguay and Argentina; Bolivia: Andean Piedmont of Santa Cruz. (890, 924, 1011, 1248, 1567, 1813, 1990, 2017, 2092, **2481**)

Gynerium Willd. ex P. Beauv.

Conert, H. J. 1961. Die Systematik und Anatomie der Arundinoideae. Cramer Verlag, Weinheim.

G. sagittatum (Aubl.) P. Beauv., Ess. Agrostogr. 138, 153, pl. 24, f. 6. 1812. *Saccharum sagittatum* Aublet, Hist. Pl. Guiane 1: 50. 1775. *G. procerum* P. Beauv., Ess. Agrostogr. 164, pl. 24, f. 6. 1812. *G. saccharoides* Humb. & Bonpl., Pl. Aequin. 2: 105, pl. 115. 1813. *Arundo saccharoides* (Humb. & Bonpl.) Poir. in Lam., Encycl. Suppl. 4: 703. 1816. *G. parviflorum* Nees, Agrost. Bras. 463. 1829.

Widespread along the banks of the Río Grande; local name: *caña brava*. Distribution: Central America to Argentina; Bolivia: the Yungas and the Beni.

Hackelochloa Kuntze

H. granularis (L.) Kuntze, Revis. Gen. Pl. 2: 776. 1891. *Cenchrus granularis* L., Mant. Pl. 2: 575. 1771. *Manisuris granularis* (L.) Sw., Prodr. 25. 1788. *Rytilix granularis* (L.) Skeels, U.S.D.A. Bull. Foreign Pl. Intr. 282: 20. 1913. *Mnesithea granularis* (L.) Koning & Sosef, Blumea 31(2): 303. 1986.

Uncommon, on gravel soils of lateritic crests in *cerrado*; flowering November to May. Distribution: throughout the tropics. (634, 892, 1487, 1615)

Hemarthria R. Brown

H. altissima (Poir.) Stapf & C. E. Hubb., Bull. Misc. Inform. 1934: 109. 1934. *Rottboellia altissima* Poir., Voy. Barbarie 2: 105. 1789. *R. fasciculata* Lam., Tabl. Encycl. 1: 204. 1791. *Manisuris altissima* (Poir.) Hitchc., J. Wash. Acad. Sci. 24: 282. 1934. *M. fasciculata* (Lam.) Hitchc., Am. J. Bot. 2: 299. 1915.

Rare, in disturbed soils of seasonally inundated savanna; palatable (3). Distribution: throughout the tropics. (1508, 1553)

Homolepis Chase

Zuloaga, F. O. & T. R. Soderstrom. 1985. Classification of the outlying species of New World *Panicum* (Poaceae: Paniceae). Smithson. Contr. Bot. 59: 1–63.

H. aturensis (H.B.K.) Chase, Proc. Biol. Soc. Wash. 24: 146. 1911. *Panicum aturense* H.B.K., Nov. Gen. Sp. 1: 103. 1816. *P. viridiflorum* Nees, Agrost. Bras. 135. 1829. *P. blepharophorum* C. Presl, Rel. Haenk. 1: 312. 1830.

Rare, streambank in forest; flowering in January. Distribution: Mexico to Brazil; Bolivia: Andean Piedmont of Santa Cruz and the Beni. (1676)

Hymenachne P. Beauv.

KEY TO SPECIES

1a. Panicle branches appressed to the axis, forming a spicate panicle; leaf blades 0.5–2(3) cm wide ..... *H. amplexicaulis*
1b. Panicle branches laxly ascending to spreading, the panicle not spicate; leaf blades (1.5)2–4 cm wide ..... *H. donacifolia*

H. amplexicaulis (Rudge) Nees, Agrost. Bras. 276. 1829. *Panicum amplexicaule* Rudge, Pl. Guian. 1: 21, t. 27. 1805. *Agrostis monostachya* Poir., Encycl. Suppl. 1: 256. 1810. *P. perdensum* Steudel, Syn. Pl. Glumac. 1: 65. 1854.

Common, roadside ponds and along banks of streams in full sunlight, especially disturbed cattle crossings; palatable (4); flowering October to April; local name: *cañuela*. Distribution: Mexico to Uruguay and Argentina; Bolivia: the Beni. (790, 1362B, 1691, 1739, 1778, 2380)

H. donacifolia (Raddi) Chase, J. Wash. Acad. Sci. 13: 177. 1923. *Panicum donacifolium* Raddi, Agrost. Bras. 44. 1823. *P. auriculatum* Willd. ex Sprengel, Syst. Veg. 1: 322. 1825. *P. cordatum* Doell in Mart., Fl. Bras. 2(3): 239. 1880. *H. auriculata* (Willd.) Chase, Proc. Biol. Soc. Wash. 21: 5. 1908. *Hymenachne cordata* (Doell) Kulhm., Comiss. Linhas Telegr. Estratég. Mato Grosso Amazonas 67, Annexo 5, Bot. 11: 45. 1922.

Similar to *H. amplexicaulis* in habit, distribution, and phenology, the two species frequently occurring in mixed populations; palatable (4); local name: *cañuela*. Distribution: Costa Rica to Paraguay and northern Argentina; Bolivia: Andean Piedmont of Santa Cruz and the Beni. (683, 1362A, 1743, 2450)

Hyparrhenia Andersson in Stapf.

Clayton, W. D. 1969. A revision of the genus *Hyparrhenia*. Royal Botanic Gardens, Kew. Additional Series II. London.

KEY TO SPECIES

1a. Spatheate sheaths subtending racemes hirsute; spikelet pairs 2–3 per raceme; lower glume of sessile spikelet with 2 medial longitudinal grooves; racemes reflexed at maturity, rachis hairs white ..... *H. bracteata*
1b. Spatheate sheaths subtending racemes glabrous; spikelet pairs 4–8 per raceme; lower glume of sessile spikelet lacking grooves; racemes ascending, rachis hairs reddish ..... *H. rufa*

H. bracteata (Willd.) Stapf in Prain, Fl. Trop. Africa 9: 360. 1919. *Andropogon bracteatus* Humb. & Bonpl. ex Willd., Sp. Pl. ed. 4. 914. 1806. *Anthistiria foliosa* H.B.K., Nov. Gen. Sp. 1: 191. 1816. *Anthistiria reflexa* H.B.K., Nov. Gen. Sp. 1: 191. 1816. *Anthistiria pilosa* J. S. Presl & C. Presl, Rel. Haenk. 1: 348. 1830. *Andropogon trachypus* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 2: 280. 1832. *Anthistiria andropogonoides* Steudel, Syn. Pl. Glumac. 1: 402. 1855.

Common, seasonally inundated savanna and savanna marsh; somewhat palatable (2), foliage coarse, but less abundant in overgrazed savanna; flowering April to (*May*) June; $2n$ = about 40. Distribution: Mexico to Brazil and tropical Africa; Bolivia: the Beni. (888, 897, 912, 2020, 2108, **2480,** 2595)

H. rufa (Nees) Stapf in Prain, Fl. Trop. Africa 9: 304. 1919. *Trachypogon rufus* Nees, Agrost. Bras. 345: 1829. *Andropogon rufus* (Nees) Kunth, Révis. Gramin. 2(39). 1832.

An important cultivated forage grass that has become naturalized throughout the region in *cerrado* communities and as a weed along roads. When seeded into degraded *cerrado*, this species will replace *Elionurus muticus* as the dominant grass if grazed lightly for two to three years; flowering *May* to July, a secondary peak of flowering in November; local name: *yaragua*. (516, 1008, 2108A)

Ichnanthus P. Beauv.

Stieber, M. T. 1982. Revision of *Ichnanthus* sect. *Ichnanthus* (Gramineae, Panicoideae). Syst. Bot. 7(1): 85–115. Stieber, M. T. 1987. Revision of *Ichnanthus* sect. *Foveolatus* (Gramineae: Panicoideae). Syst. Bot. 12: 187–216.

KEY TO SPECIES

1a. Leaf blades 3–5 mm wide; panicles 5–10 cm long; branches with 3–8 spikelets clustered on

the lower side of the midportion of the branches, and a single long-pedicellate spikelet at apex ..... *I. procurrens*

1b. Leaf blades 5–20 mm wide; panicles 10–40 cm long, spikelets irregularly arranged along the branches.
2a. Paired winglike appendages at base of upper floret present; blades stiffly spreading, usually velutinous; culms stout ..... *I. inconstans*
2b. Paired appendages lacking (scars only); blades lax, usually glabrous; culms not stout ..... *I. pallens*

I. inconstans (Trin. ex Nees) Doell in Mart., Fl. Bras. 2(2): 287. 1877. *Panicum inconstans* Trin. ex Nees, Agrost. Bras. 132. 1829. *I. velutinus* Ekman, Ark. Bot. 13: 31, p. 2, f. 2. 1913. *I. peruvianus* Mez, Feddes Repert. Spec. Nov. Regni Veg. 15: 129. 1918. *I. polycladus* Mez, Feddes Repert. Spec. Nov. Regni Veg. 15: 129. 1918; see Stieber (1987) for extensive synonymy.

Common, rooting in organic soils of cracks on granitic or sandstone outcrops, rarely in *cerrado* or scrub; palatable (3); flowering January (*February*) to April and irregularly throughout the year; $2n = 20$. Distribution: Peru, Brazil, Paraguay, and Argentina; Bolivia: the Yungas. (1449, 1731, 1818, 1975, **2331,** 2782B)

I. pallens (Sw.) Munro ex Benth., Fl. Hongk. 414. 1861. *P. pallens* Sw., Prod. 23. 1877. *I. axillare* (Nees) Hitchc. & Chase, Contr. U.S. Natl. Herb. 18: 334. 1917. *I. tipuaniensis* Rogers, Phytologia 26: 59–64. 1973; see Stieber (1982) for extensive synonymy.

Occasional, forming colonies in humid soils of forest and as a weed following shifting agriculture; palatable (4); flowering November to May. Distribution: throughout the tropics. (1376, 2104, 2448)

I. procurrens (Nees ex Trin.) Swallen, Phytologia 11: 149. 1964. *P. procurrens* Nees ex Trin., Gram. Panic. 183. 1826. *Echinolaena procurrens* (Nees ex Trin.) Kunth, Révis. Gramin. 1: 54. 1829.

Common, valley-side *campo* (upslope to downslope), seasonally humid to inundated savanna and savanna marsh, rarely in *cerrado*; unpalatable (0); flowering September (*January*) to July; $2n = 20$. Distribution: Venezuela, Brazil, Paraguay, and Argentina; Bolivia: Andean Piedmont of Santa Cruz and the Beni. (591, 612, 631, 712, 776, 1424, 1642, **2285,** 2590; *Thomas 5652, 5671* NY, LPB)

Imperata Cyrillo

Gabel, M. L. 1982. A systematic study of the genus *Imperata* (Gramineae: Andropogoneae). Ph.D. Dissertation. Iowa State Univ., Ames, Iowa.

KEY TO SPECIES

1a. Inflorescence 7–12 cm long; base of blades as wide as the apex of the sheath, not narrowed to a thickened, indurate midrib ..... *I. brasiliensis*
1b. Inflorescence 15–30 cm long; base of blades narrower than the apex of the sheath, reduced to a thickened, indurate midrib.
2a. Lower panicle branches 3–10 cm long; the narrowed base of the blade 5–10 cm long ..... *I. contracta*
2b. Lower panicle branches 1–2 cm long; the narrowed base of the blade about 1 cm long ..... *I. tenuis*

I. brasiliensis Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 2: 331. 1832. *Saccharum sape* St. Hil., Voy. Distr. Diam. 1: 386. 1833. *I. brasiliensis* var. *mexicana* Rupr., Mém. Acad. Roy. Sci. Bruxelles Bel. 9: 245. 1842. *I. sape* (St. Hil.) Anderss., Ofvers. Förh. Köngl. Svenska Vetensk.-Akad. 12: 160. 1855. *I. arundinacea* var. *americana* Anderss., Ofvers. Förh. Köngl. Svenska Vetensk.-Akad. 12: 160. 1855. *I caudata* Chapman, Fl. South. U.S., 2nd edition. 1883.

Abundant, forming colonies in densely wooded *cerrado* and on *cerrado*/forest margins, occasionally in *campo cerrado*; a common weed of pastures and roadsides, becoming a serious pest in banana and coffee plantations. Unpalatable (0); flowering is dependent upon fire; $2n = 20$; local name: *sujo*. Distribution: southern United States to Argentina; Bolivia: Andean Piedmont of Santa Cruz and the Beni. (1171, **2192,** 2217)

I. contracta (H.B.K.) Hitchc., Ann. Rep. Missouri Bot. Garden 4: 146. 1893. *Saccharum contractum* H.B.K., Nov. Gen. Sp. 1: 182. 1816. *S. dubium* H.B.K., Nov. Gen. Sp. 1: 183. 1816. *S. caudata* G. Meyer, Prim. Fl. Esseq. 68. 1818. *I. caudata* (G. Meyer) Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 2: 331. 1832. *Anatherum berterianum* Sprengel ex Schultes, Mant. 2: 443. 1824. *I. exaltata* var. *caudata* Hack. in DC., Monogr. Phan. 6: 99. 1889. *I. longifolium* Pilger, Bot. Jahrb. Syst. 30: 136. 1901.

Not yet collected in Chiquitanía but a zonal dominant of shallowly inundated savannas in the

Beni; probably unpalatable; flowering in July. Distribution: Mexico to Argentina. (2607)

I. tenuis Hack. in A. DC., Monogr. Phan. 6: 689. 1889. *I. exaltata* var. *angustifolius* Hack. in A. DC., Monogr. Phan. 6: 99. 1889.

Common, valley-side *campo* (midslope to downslope), seasonally humid and inundated savanna and savanna marsh; unpalatable (0); flowering December to (*February*) June. Distribution: central Brazil and northeastern Argentina; Bolivia: Andean Piedmont of Santa Cruz and the Beni. (655, 719, 768, 818, 961, 1129, 1580, 1808, 1872, 2117, 2482, 2605)

Lasiacis (Griseb.) Hitchc.

Davidse, G. 1978. A systematic study of the genus *Lasiacis* (Gramineae: Paniceae). Ann. Missouri Bot. Gard. 65: 1133–1254.

KEY TO SPECIES

1a. Panicle branches reflexed; sheaths glabrous ..... *L. ligulata*
1b. Panicle branches ascending or spreading, sheaths papillose-hispid ..... *L. sorghoidea*

L. sorghoidea (Desv.) Hitchc., Contr. U.S. Natl. Herb. 18: 338. 1917. *Panicum lanatum* Sw., Prodr. 24. 1788, non Rottb., 1778. *P. sorghoidea* Desv. in Ham., Prodr. Pl. Ind. Occ. 10. 1825. *L. guaraniticum* (Speg.) L. Parodi, Notas Mus. La Plata, Bot. 8: 95. 1943; an extensive synonymy is given in Davidse (1978).

Common, seasonal forest and forest/savanna margins, forming robust colonies along new roads in forest; very palatable (4), an important source of forage in the dry season when most savanna grasses are senescent; flowering January to July; $2n = 36$; local name: *taquarilla*. Distribution: Mexico to Argentina; Bolivia: Andean Piedmont of Santa Cruz, Cochabamba, and the Yungas. (553, 675, 883, 906, 1888, 2014, 2099, **2332**)

L. ligulata Hitchc. & Chase, Contr. U.S. Natl. Herb. 18: 337. 1917.

Occasional, forest openings and margins. Distribution: West Indies, northern South America and Brazil; Bolivia: the Yungas. (965, 1000)

Leersia Sw.

Pyrah, G. L. 1969. Taxonomic and distributional studies in *Leersia* (Gramineae). Iowa State J. Sci. 44: 215–270.

L. hexandra Sw., Prodr. 21. 1788. *L. mexicana* H.B.K., Nov. Gen. Sp. 1: 195. 1816. *L. contracta* Nees, Agrost. Bras. 516. 1829. *L. glaberrima* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 5: 172. 1840. *Oryza hexandra* (Sw.) Doell in Mart., Fl. Bras. 2(2): 10. 1877.

Common, forming colonies in shallow lakes, seasonal ponds, and seasonally inundated savannas; very palatable (4), savanna wetlands with a high proportion of this species are prized by ranchers; flowering in *March*, *April*, and irregularly throughout the year; populations are largely infertile (seed set <5%); $2n = 48$; local name: *arrocilla*. Distribution: throughout the tropics. (701, 762, 815, 943, 1635, 1777, 2023, **2416**)

Leptochloa P. Beauv.

KEY TO SPECIES

1a. Lemma papillose, strongly laterally compressed, glabrous or sparsely pilose on back, the margins pilose on upper half, awned or awnless; glumes lanceolate; spikes distinctly 2-ranked ..... *L. virgata*
1b. Lemma not papillose, dorsally compressed, glabrous on back, the margins pilose on lower ⅓, mucronate, acute, or irregularly lobed; glumes ovate or oblong; spikes obscurely 2-ranked or secund.
2a. Apex of lemma irregularly toothed or lobed, the midnerve forming a mucro; spikelets obscurely 2-ranked; racemes 10–20 per panicle ..... *L. uninervia*
2b. Apex of lemma entire, acute or mucronate but not irregularly toothed or lobed; spikelets distinctly secund; racemes 20–40 per panicle ..... *L. scabra*

L. uninervia (C. Presl) Hitchc. & Chase, Contr. U.S. Natl. Herb. 18: 383. 1917. *Megastachya uninervia* C. Presl, Rel. Haenk. 1: 283. 1830. *Diplachne uninervia* (C. Presl) Parodi, Univ. Nac. Buenos Aires Revista Centr. Estud. 18: 147. 1925. *D. tarapacana* Phil., Anales Mus. Nac. Chile Bot. 8: 88. 1891. *D. carinata* Hack., Bol. Acad. Ci. (Córdoba) 16: 253. 1900.

An extremely variable taxon similar to and possibly not distinct from *L. fascicularis* (Lam.) A. Gray. Occasional, as a weed in seasonal ponds and roadside ditches. Distribution: United States to Argentina; Bolivia: Andean Piedmont of Santa Cruz, Beni, and Cochabamba. (825, 1712)

L. scabra Nees, Agrost. Bras. 435. 1829.

Occasional, roadside ditches in standing water; flowering November to February. Distribution: southern United States to Brazil. (1425, 2300)

L. virgata (L.) P. Beauv., Ess. Agrostogr. 71, 166. 1812. *Cynosurus virgatus* L., Syst. Nat. ed. 10. 2: 876. 1759. *Chloris digitaria* H.B.K., Nov. Gen. Sp. 1: 168. 1816. *L. digitaria* (H.B.K.) Nees, Agrost. Bras. 433. 1829. *L. gracilis* (H.B.K.) Nees, Syll. Pl. Ratisb. 1: 4. 1824. *L. domingensis* (Jacq.) Trin., Fund. Agrost. 133. 1820. *L. barbata* Desv., Opusc. Sci. Phys. Nat. 104. 1831. *L. mutica* Steudel, Syn. Pl. Glumac. 1: 208. 1854. *L. villosa* Ekman, Ark. Bot. 10(7): 31, p. 3, 6. 1911.

Common, roadside weed in forest soils; flowering throughout the year. Distribution: southern United States to northern Argentina; Bolivia: Andean Piedmont of Santa Cruz and the Yungas. (602, 607, 639, 827, 828, 840, 973, 1261, 1312, 1567A, 1681, 1708, 2298)

Leptocoryphium Nees

L. lanatum (H.B.K.) Nees, Agrost. Bras. 84. 1829. *Paspalum lanatum* H.B.K., Nov. Gen. Sp. 1: 94, t. 29. 1816. *L. molle* Nees, Agrost. Bras. 85. 1829. *Anthaenantia lanata* (H.B.K.) Benth., J. Linn. Soc. Bot. 19: 39. 1881. *Milium juncoides* Speg., An. Soc. Cient. Argent. 16: 105. 1883.

Occasional in *cerrado*, zonally abundant in sandy soils in valley-side *campos* (upslope); flowering is dependent upon fire; $2n = 20$. Distribution: Central America to Argentina; Bolivia: Andean Piedmont of Santa Cruz, Beni, and the Yungas. (781, 1111, 1163, 1368, 1430, 1455, 1660, **2190**, 2768, 2784; *Thomas 5630* NY, LPB)

Loudetia Hochst. ex A. Braun

L. flammida (Trin.) C. E. Hubb., Bull. Misc. Inform. 1936: 361. 1936. *Arundinella flammida* Trin., Sp. Gram. 3: 267. 1831. *Trichopteryx flammida* (Trin.) Benth., J. Linn. Soc., Bot. 19: 59. 1882.

Common, in savanna marsh, seasonally humid, and seasonally inundated savanna; characteristic of valley-side *campos* where it displays a bimodal distribution at the top and bottom of the soil-moisture gradient (but absent midslope); moderately palatable (2); flowering January (*February*) to May; $2n = 20$. Distribution: Brazil and Paraguay; Bolivia: Andean Piedmont of Santa Cruz and the Yungas. (718, 757, 905, 1747, 1861, **2324**)

Loudetiopsis Conert

L. chrysothrix (Nees) Conert, Bot. Jahrb. Syst. 77: 285. 1957. *Tristachya chrysothrix* Nees, Agrost. Bras. 460. 1829.

Eiten (1972) reported this species to be characteristic of *cerrado* communities in central Brazil, and it is common in the dry savannas of the Andean foothills near Samaipata, Santa Cruz (1,500 m). However, it is rare in Chiquitanía and restricted to seasonally humid savannas with sandy soils; flowering in January and February. Distribution: Brazil and Paraguay. (791, 1666, 1738, 1834, 2488)

Luziola Juss. ex Gmel.

Swallen, J. R. 1965. The grass genus *Luziola*. Ann. Missouri Bot. Gard. 52: 472–475.

KEY TO SPECIES

1a. Achene striate; pistillate glumes pleated when immature; pistillate panicle with racemose branches, the pedicels appressed to ascending ..... *L. bahiensis*

1b. Achene smooth; pistillate glumes not pleated; pistillate panicle open, freely branched, the pedicel spreading ..... *L. peruvianum*

L. bahiensis (Steudel) Hitchc., Contr. U.S. Natl. Herb. 12: 234. 1909. *Caryochloa bahiensis* Steudel, Syn. Pl. Glumac. 5. 1854. *L. longivalvula* Doell in Mart., Fl. Bras. 2(2): 17. 1871. *L. striata* Bal. & Poit., Bull. Soc. Hist. Nat. Toulouse 12: 231, t. 4, f. 2. 1878. *L. pusilla* S. Moore, Trans. Linn. Soc. Bot. II. 4: 507, t. 37, f. 1–8. 1895. *L. contracta* Hack., Oesterr. Bot. Z. 52: 8. 1902.

Common, in savanna marsh growing underneath the robust dominant *Saccharum trinii*; flowering November (*December*) to July, possibly stimulated by fire. Distribution: southern United States to Argentina. (622, 1026, 1422, 1647, 1780, 2250)

L. peruvianum Juss. ex Gmel., Syst. Nat. 2: 637. 1791. *L. mexicana* H.B.K., Nov. Gen. Sp. 1: 199. 1816. *Milium natans* Spreng., Syst. Veg. 1: 250. 1825. *L. brasiliana* Moric., Pl. Nouv. Amér. 94, t. 60, 1840. *L. leiocarpa* Lindman, Köngl. Svenska Vetensk. Akad. Handl. 34(6): 12. 1900. *L. doelliana* Prodoehl, Bot. Arch. 1: 240. 1922.

Common, in seasonal ponds and occasionally in seasonally inundated savanna; palatable (4); flowering October to (*January*) May. Distribution: southern United States to Argentina; Bolivia: Tarija, Andean Piedmont of Santa Cruz, and the Beni. (850, 1244, 1648, 2085, 2283, 2288)

Melinis P. Beauv.

M. minutiflora P. Beauv., Ess. Agrostogr. 54. 1812. *Panicum melinis* var. *inerme* Doell in Mart., Fl. Bras. 2(2): 242. 1877.

Although occurring as a roadside weed in humid montane regions of Bolivia, in Chiquitanía it is a naturalized species characteristic of bromeliad thickets on granitic outcrops; its highly aromatic and glandular foliage makes it very palatable to cattle (4); flowering in *May*; local name: *capim ceroso*. Distribution: throughout the tropics. (933, 2102)

Mesosetum Steudel

Filgueiras, T. de S. 1986. O gênero *Mesosetum* Steudel (Gramineae: Paniceae). Thesis. Universidad Estadual de Campinas, S.P., Brasil. Swallen, J. R. 1937. The grass genus *Mesosetum*. Brittonia 2: 363–392.

M. cayennense Steudel, Syn. Pl. Glumac. 118. 1854.

Occasional, superficial soils on granitic outcrops, rarely in gravel soils of *cerrado* (*campo limpo*) or *campo rupestre*; flowering April to September. Distribution: West Indies to Brazil. (908, 1217, 1491, 1981)

Microchloa R. Brown

M. indica (L.f.) P. Beauv., Ess. Agrostogr. 115, t. 20, f. 8. 1812. *Nardus indica* L. f., Suppl. Pl. 105. 1781.

Common, superficial soils over granitic outcrops; rarely on lateritic outcrops in *cerrado*; flowering November to May. Distribution: throughout the tropics; Bolivia: Cochabamba and the Yungas. (799, 1443, 1484, 1547, 1782, 1826, 2091)

Olyra L.

Zuloaga, F. O. & T. R. Soderstrom. 1989. A revision of the genus *Olyra* and the new segregate genus *Parodiolyra* (Poaceae: Bambusoideae: Olyreae). Smithson. Contr. Bot. 69: 1–79.

KEY TO SPECIES

1a. Pistillate floret pubescent; lower glume long-aristate; lower panicle branches lacking pistillate spikelets ..... *O. ciliatifolia*
1b. Pistillate floret glabrous; lower glume short-aristate to acuminate; all panicle branches with pistillate spikelets.
  2a. Panicle more or less branched, the branches alternate; pistillate spikelets 1–2 per inflorescence branch, the florets ovate and smooth ..... *O. latifolia*
  2b. Panicle of 4–8 verticillate racemes inserted at 1–2 nodes; pistillate spikelets and florets various.
    3a. Pistillate spikelets (2)3–4 per raceme, the florets narrowly elliptic and distinctly pitted ..... *O. fasciculata*
    3b. Pistillate spikelets 1–2 per raceme, the florets ovate and smooth *O. caudata*

O. caudata Trin., Linnaea 10: 292. 1836. *O. dimidiata* Hochstetter ex Steudel, Syn. Pl. Glum. 1: 36. 1853. *O. pittieri* Hack., Oesterr. Bot. Z. 51: 461. 1901.

Rare, forest at Parque Nacional "Noel Kempff Mercado." (*Thomas 5734* NY)

O. ciliatifolia Raddi, Agrost. Bras. 19. 1823. *O. cuneatifolia* Desv., Opusc. Sci. Phys. Nat. 106. 1831.

Occasional, *cerrado*/forest margins and transitional scrub; palatable (2); flowering December to April; $2n = 44$; local name: *taquarilla*. Distribution: northern South America to Brazil and Paraguay; Bolivia: the Beni. (649, 728, 869, 1614, 1889, 1920, **2386**)

O. fasciculata Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 3: 113. 1835. *O. heliconia* Lindman, Köngl. Svenska Vetensk. Acad. Handl. 34(6): 11. 1900.

Uncommon, in deep shade of seasonal forest, rarely as a weed along roads in forest soils; flowering October to December; local name: *taquarilla*. Distribution: Peru and Brazil; Bolivia: Andean Piedmont of Santa Cruz and the Yungas. (671, 1377, 2385, 2828)

O. latifolia L., Syst. Nat. ed. 10. 2: 1261. 1759. *O. arundinacea* H.B.K., Nov. Gen. Sp. 1: 197. 1816. *O. cordifolia* H.B.K., Nov. Gen. Sp. 1: 198. 1816. *O. pubescens* Raddi, Agrost. Bras. 18. 1823. *O. scabra* Nees, Agrost. Bras. 306. 1829. *O. brasiliensis* Desv., Opusc. 106. 1831. *O. media* Desv., Opsuc. 106. 1831.

Occasional, seasonal forest and forest openings, locally abundant in gallery forest and along streams in seasonal forest; flowering November to July; local name: *taquarilla*. Distribution: Mexico to Argentina; Bolivia: Beni and the Yungas. (554, 677, 931, 1047, 1379, 1496, 1774, 1969, 2013)

Oplismenus P. Beauv.

Scholz, U. 1981. Monographie der Gattung *Oplismenus*. Phanerogamarum Monographiae Tomus XII. J. Cramer, Vaduz. Davey, J. C. & W. D. Clayton. 1978. Some multiple discrim-

inant function studies on *Oplismenus* (Gramineae). Kew Bull. 33(1): 147–157.

KEY TO SPECIES

1a. Awn antrorsely scabrous; racemes hispid ..... *O. burmannii*
1b. Awn smooth; racemes not hispid ..... *O. hirtellus*

O. burmanni (Retz.) P. Beauv., Ess. Agrostogr. 54. 1812. *Panicum burmanni* Retz., Observ. Bot. 3: 10. 1783.

Rare, granitic outcrop; flowering in May. Distribution: throughout the tropics. (939)

O. hirtellus (L.) P. Beauv., Ess. Agrostogr. 54. 1812. *Panicum hirtellum* L., Syst. Nat. ed. 10. 870. 1759. *P. setarium* Lam., Tabl. Encycl. 1: 170. 1791. *O. setarius* (Lam.) Roemer & Schultes, Syst. Veg. 2: 481. 1817. *O. brasiliensis* Raddi, Agrost. Bras. 40. 1823. *O. velutinum* (G. Meyer) Schultes, Mant. 2. 271. 1824.

Sometimes treated as two species (*O. setarius*), but the two forms intergrade and share the same habitat. Common in forest, especially where disturbed by cattle; palatable (3); flowering January to (*April*) July. Distribution: United States to Argentina; Bolivia: Andean Piedmont of Santa Cruz, Chapare, the Yungas, and the Beni. (693, 750, 1030, 1881, 1886, 1967, 2002, 2009, 2030, 2074)

Orthoclada P. Beauv.

O. laxa (L. Rich.) P. Beauv., Ess. Agrostogr. 70, 149, 168. 1812. *Aira laxa* L. Rich., Actes Soc. Hist. Nat. Paris 1: 106. 1792.

Not yet collected in Chiquitanía but found in forest islands in the Beni. Distribution: Mexico to Brazil.

Oryza L.

Tateoka, T. 1962. Taxonomic studies of *Oryza* I. *O. latifolia* complex. Bot. Mag. Tokyo 75(893): 418–427. Tateoka, T. 1962. Taxonomic studies of *Oryza* II. Several species complexes. Bot. Mag. Tokyo 75(894): 455–461. Tateoka, T. 1963. Taxonomic studies of *Oryza* III. Key to species and their enumeration. Bot. Mag. Tokyo 76(899): 165–173.

KEY TO SPECIES

1a. Glumelike bracts about as long as the spikelet ..... *O. grandiglumis*
1b. Glumelike bracts less than ¼ the length of the spikelet.
2a. Spikelets whitish green at maturity (rarely reddish), 5–6(7) mm long, erect on the pedicels; lemma muticate or aristate, the awns up to 2 cm long ..... *O. latifolia*
2b. Spikelets reddish or tan at maturity, 7–10 mm long, obliquely inserted on pedicels.
3a. Awn 4–10 cm long; spikelets oblong, 9–10 mm long, spikelets deciduous ..... *O. rufipogon*
3b. Awn absent or up to 2 cm long; spikelets elliptic to oblong, 7–9 mm long, spikelets persistent ..... *O. sativa*

O. grandiglumis (Doell) Prodoehl, Bot. Arch. 1: 233. 1922. *O. sativa* var. *grandiglumis* Doell in Mart., Fl. Bras. 2(2): 8. 1871. *O. latifolia* var. *grandiglumis* (Doell) A. Chev., Rev. Int. Bot. Appl. Agric. Trop. 12: 1207. 1932.

Occasional, along streams in forest, especially where light intensity is high; flowering throughout the year; $2n = 48$. Distribution: northern South America, Peru, and Brazil. (922, 1052, 1677, **2232**)

O. latifolia Desv., J. Bot. 1: 77. 1813. *O. sativa* L. var. *latifolia* (Desv.) Doell in Mart., Fl. Bras. 2(2): 7. 1871. *O. platyphylla* J. A. Schultes & J. H. Schultes, Syst. Veg. 7: 1364. 1830.

Rare, roadside ditches in forest soils. Distribution: Mexico to northern Argentina; Bolivia: Andean Piedmont of Santa Cruz and the Beni. (691)

O. rufipogon Griffiths, Ic. Pl. Asiat. 3: 5, pl. 144, f. 2. 1851. *O. glumipatula* Steudel, Syn. Pl. Glumac. 1: 3. 1854. *O. perennis* Moench sensu Hitchcock, Grasses W. Ind. 145. 1936. *O. paraguayensis* Wedd. ex Fourn., Compt. Rend. Cong. Int. Bot. & Hort. Paris 1878: 233. 1880. *O. sativa* var. *paraguayensis* L. Parodi, Physis 11: 244. 1933.

Commonly collected in Amazonia along river banks, where it is a floating aquatic of indefinite duration with caulescent foliage; however, in Chiquitanía it occurs as a caespitose perennial with basal foliage. Common, seasonal ponds of *pantanal* complex, rarely in seasonally inundated savanna and small pools on granitic outcrops; palatable (4); flowering April (*May*) to August. Distribution: throughout the tropics. (941, 1894, 2086)

O. sativa L., Sp. Pl. 333. 1753.

Cultivated, usually interplanted with maize; a staple of the local diet.

Otachyrium Nees

Sedulsky, T. & T. R. Soderstrom. 1984. Revision of the genus *Otachyrium* (Poaceae: Panicoideae). Smithson. Contr. Bot. 57: 1–24.

O. versicolor (Doell) Henrard, Blumea 4: 511. 1941. *Panicum truncatum* Nees, Agrost. Bras. 215. 1829, non Trin., 1826. *P. versicolor* Doell in Mart., Fl. Bras. 2(2): 254. 1877.

Plants variable between populations for spikelet size and morphology. Locally abundant in shallowly inundated or seasonally humid savanna, rarely in low forest scrub (San José de Chiquitos); palatable (2–3); flowering is stimulated by (but not dependent upon) fire, August to May. Distribution: Colombia, Venezuela, the Guianas, Brazil, and Paraguay; Bolivia: Andean Piedmont of Santa Cruz and the Beni. (864, 1197, 1522, 1623, 1724, 2769)

Panicum L.

Zuloaga, F. O. 1986. Systematics of new world species of *Panicum* (Poaceae: Paniceae). Pp. 287–309 *in* T. R. Soderstrom, K. W. Hilu, C. S. Campbell & M. E. Barkworth (editors), Grass Systematics and Evolution. Smithsonian Institution, Washington, D.C.

KEY TO SPECIES

1a. Spikelets 5–7 mm long; panicles open, disarticulating at the base of the peduncle at maturity; the base of the upper florets with paired tufts of thick hairs ..... *P. olyroides*
1b. Spikelets 1–3 mm long; panicles open, narrowly elliptic, spicate, or racemose; the base of the upper florets lacking tufts of thick hairs.
2a. Lowermost panicle branches verticillate.
3a. Upper floret rugose, only the lowermost branches verticillate; caespitose perennial ..... *P. maximum*
3b. Upper floret smooth, the panicle branches verticillate at all the nodes; culms decumbent and rooting at the nodes ..... *P. mertensii*
2b. Panicle branches alternate or subopposite, not verticillate, if several inserted at a single node, then borne on one side and of unequal size.
4a. Glumes and lower lemma vesciculate-pubescent; upper lemma minutely rugose.
5a. Primary panicle branches bearing spikelets to the base, bearing 1–3 secondary panicle branches; pedicels spreading to ascending, 1–5 mm long ..... *P. millegrana*
5b. Primary panicle branches lacking spikelets on lower ½–⅓, unbranched; pedicels uniformly short, 0.5–2 mm long and appressed to branches ..... *P. sellowii*
4b. Glumes and lower lemma glabrous or puberulent but not vesciculate-pubescent; upper lemma smooth.
6a. Panicles 2 from each of the upper nodes, overlapping, the bases included in the sheath; sheaths usually coarsely hispid; decumbent annuals.
7a. Spikelets about 3 mm long, the glumes and lower lemma acuminate, the floret ovate to elliptic ..... *P. rudgei*
7b. Spikelets about 2 mm long, the glumes and lower lemma acute, the floret elliptic to suborbicular ..... *P. cayennense*
6b. Panicle 1 from each node, axillary inflorescences (if present) on short leafy branches; sheaths variously glabrous to pubescent but not coarsely hispid; annuals or perennials.
8a. Lower glume ½–¾ the length of spikelet, the apex blunt or rounded; foliage cauline and uniformly distributed on the culms; plants stoloniferous or decumbent and rooting at the nodes.
9a. Spikelets 1.8–2.2 mm long.
10a. Leaf blades velutinous (at least abaxially), lax; panicle of 2–5 racemose branches, pyramidal ..... *P. pantrichum*
10b. Leaf blades glabrous, strictly ascending to erect; panicle freely branched, globose ..... *P. schwackeanum*
9b. Spikelets 1.2–1.5 mm long.
11a. Panicles about 7 × 7 cm; leaf blades ≥ 5 cm long ..... *P. cyanescens*
11b. Panicles about 3 × 3 cm; leaf blades 2–4 cm long ..... *P. parviflorum*
8b. Lower glume up to ½ the length of the spikelet, the apex acute (somewhat blunt in *P. dichotomiflorum*); foliage basal or cauline; plants caespitose, rhizomatous, or stoloniferous.
12a. Back of lower lemma with paired, glandular pits ..... *P. pulchellum*
12b. Back of lower lemma not glandular-pitted.
13a. Panicles spicate, the spikelets 6–25, borne on short, erect, appressed branches; plants caespitose, sedgelike, bunch grasses.
14a. Spikelets 10–25, 1.5–1.8 mm long; rachilla internode elongate; foliage usually glabrous ..... *P. stenodes*
14b. Spikelets 5–10, 2.2–2.8 mm long; rachilla internode not elongate; foliage usually pubescent ..... *P. caricoides*
13b. Panicles not spicate; spikelets numerous or if few, then the branches spreading; plant habit various 15

15a. Spikelets 1–1.5 mm long.
16a. Lower glume reduced to a membranous, nerveless scale ..... *P. trichanthum*
16b. Lower glume well developed, 1–5-nerved.
17a. Lower lemma lacking a palea.
18a. Lower glume gibbous, loosely clasping the spikelet; panicles narrowly elliptic, the spikelets ovate, ascending; nodes glabrous ..... *P. scabridum*
18b. Lower glume not gibbous, tightly clasping the spikelet; panicles pyramidal, the branches racemose, the spikelets lanceolate, secund; nodes bearded ..... *P. polygonatum*
17b. Lower lemma with a well-developed palea.
19a. Spikelets 1–1.2 mm long; leaf blades ovate; panicles open, diffuse ..... *P. trichoides*
19b. Spikelets about 1.5 mm long; leaf blades linear to lanceolate; primary panicle branches sparsely branched, racemose.
20a. Spikelets uniformly distributed on a pilose rachis ..... *P. pilosum*
20b. Spikelets irregularly distributed on a glabrous rachis.
21a. Culms stout, about 5 mm in diameter; leaf blades cordate and clasping the culm at base ..... *P. hylaeicum*
21b. Culms 1–2 mm in diameter; leaf blades not cordate-clasping at the base ..... *P. laxum*

15b. Spikelets 2–3 mm long.
22a. Lower glume ¼–⅓ the length of spikelet, 1-nerved, the apex broadly acute to truncate; anthers bright orange when fresh ..... *P. dichotomiflorum*
22b. Lower glume about ½ the length of the spikelet, acute to acuminate, 3–5-nerved; anthers variously colored, usually yellow or purple.
23a. Inflorescence a panicle of secund racemes ..... *P. stoloniferum*
23b. Inflorescence an open or narrowly elliptic panicle.
24a. Leaf blades lanceolate, acuminate; plants of shaded habitats ..... *P. haenkeanum*
24b. Leaf blades linear; heliophytes.
25a. Upper florets dark chestnut brown, rotated 90° in the spikelet; foliage basal.
26a. Bracts subtending the upper floret 5: 2 glumes, 2 lower lemmas, and a palea ..... *P. quadriglume*
26b. Bracts subtending the upper floret 4: 2 glumes, 1 lower lemma, and a palea ..... *P. peladoense*
25b. Upper florets stramineous to dull brown, not rotated 90°; foliage cauline.
27a. Plants robust, 1.5–2 m tall, rhizomatous perennials; culms brittle; leaf blades deciduous; pedicels ascending ..... *P. tricholaenoides*
27b. Plants 30–50 cm tall, caespitose or decumbent annuals; culms not brittle; leaves not caducous; pedicels divergent ..... *P. hirticaule*

P. caricoides Nees ex Trin., Gram. Panic. 149. 1826. *P. stenodoides* Hubb., Proc. Amer. Acad. Arts. 49: 497. 1913. *P. junciforme* Steudel, Syn. Pl. Glumac. 1: 82. 1854, nomen nudum.

Easily confused with *P. stenodes*, which grows in more humid or seasonally inundated habitats; both species have been observed growing in adjacent savanna patches without evidence of introgression (2824 vs. 2825 and 2263 vs. 2268, 2269). Common, seasonally humid savanna and valley-side *campos* (upslope); flowering September to January, flowering is stimulated by (but not dependent upon) fire. Distribution: Central America, the West Indies to Brazil. (1373, 2263, 2824)

P. cayennense Lam., Tabl. Encycl. 1: 173. 1791. *P. pedunculare* Willd. ex Steudel, Nomencl. Bot. 2(10): 260. 1841.

Rare, *cerrado* and superficial sandy soil over granitic outcrops; flowering November to January. Distribution: Mexico to Argentina; Bolivia: Andean Piedmont of Santa Cruz and the Beni. (797, 1486)

P. cyanescens Nees in Trin., Gram. Panic. 202. 1826. *P. carannense* Mez, Notizbl. Bot. Gart. Berlin-Dahlem 7: 73. 1917.

Uncommon, seasonally humid savannas; flowering *January* to July. Distribution: northern South America to Argentina; Bolivia: Andean Piedmont of Santa Cruz. (1096, 1658; *Bruderreck 122* ISC, LPB)

P. dichotomiflorum Michx., Fl. Bor. Amer. 1: 48. 1803. *P. chloroticum* Nees in Trin., Gram. Panic. 236. 1826. *P. proliferum* var. *richardii* Doell in Mart. Fl. Bras. 2(2): 200. 1877. *P. proliferum* var. *xanthochlorum* Hack. ex Bertoni, Anales Ci. Parag., Ser. 2. 150. 1918; see Zuloaga (1986) for extensive synonymy.

Common in seasonal ponds on granitic outcrops and shallow roadside ditches, occasional in season-

ally inundated savanna, and rarely as a weed along roadsides in dry gravel soils; flowering November to February. Distribution: United States to Argentina; Bolivia: Andean Piedmont of Santa Cruz and the Beni. (648, 756, 1504, 1626, 1735)

P. haenkeanum C. Presl, Rel. Haenk. 1: 304. 1830. *P. costaricensis* Hack., Oesterr. Bot. Z. 51: 428. 1901.

Central American specimens are much more robust and have larger panicles than specimens collected in Bolivia and Brazil; however, spikelet morphology and the shape of the leaf blade are characteristic. Rare, in diffuse light of *Orbignya* forest; flowering in August. Distribution: Central America and Brazil. (1094)

P. hirticaule C. Presl, Rel. Haenk. 1: 308. 1830. *P. flabellatum* Fourn., Bull. Soc. Bot. France II. 27: 293. 1880, non Steudel, 1854. *P. caatingense* Renv., Kew Bull. 37: 325. 1982.

Rare, as a weed in pastures and roadsides in humid soils near San José de Chiquitos; flowering in February. Distribution: United States to Argentina; Bolivia: Andean Piedmont of Santa Cruz and the Beni. (1702, 1711)

P. hylaeicum Mez, Notizbl. Bot. Gart. Berlin-Dahlem 7: 75. 1917. *P. minutiflorum* Doell in Mart., Fl. Bras. 2(2): 253. 1877, non Rasp., 1825. *P. laxum* var. *pubescens* Doell in Mart., Fl. Bras. 2(2): 213. 1877, in part. *P. laxum* var. *amplissimum* Hack., Feddes Repert. Spec. Nov. Regni Veg. 6: 343. 1909. *P. doelli* Mez, Bot. Jahrb. Syst. 56(125): 27. 1934. *P. boliviense* Hack. sensu Smith, Wasshausen & Klein, Fl. Ilustr. Catarinense (Gramineas). 671. 1982.

Rare, roadside ditch in forest soils; flowering in November. Distribution: northern South America to Paraguay. (1426)

P. laxum Sw., Podr. 23. 1788. *P. agrostidiforme* Lam., Tabl. Encycl. 1: 172. 1791; see Zuloaga (1987) for extensive synonymy.

Plants are variable within and between populations for stature and inflorescence morphology. This grass is abundantly represented as a constituent of seasonally inundated savannas, seasonal ponds, and as a weed in roadside ditches; it is rarely found in savanna marsh and valley-side *campos*. An important source of forage, especially in abused savanna wetlands, as this species colonizes openings in the herbaceous canopy caused by cattle trampling; palatable (4); flowering throughout the year but more abundantly during the rainy season. Distribution: Mexico and the West Indies to Argentina; Bolivia: Andean Piedmont of Santa Cruz, Chapare, Beni and the Yungas. (609, 628, 632, 641, 647, 657, 727, 755, 774, 775, 813, 851, 1063, 1124, 1554, 1575, 1625, 1686, 1687, 1716, 1717, 2286, 2294, 2316, 2587)

P. maximum Jacq., Coll. Bot. 1: 76. 1786. *P. jumentorum* Pers., Syn. Pl. 1: 83. 1805. *P. praticola* Salzm. ex Doell in Mart., Fl. Bras. 2(2): 203. 1877.

A productive, high quality, cultivated, forage grass adapted to forest soils. The traditional variety (*hierba guinea*) is a robust plant reaching 2.5 m in height, newly introduced dwarf cultivars (*panico verde*, *panico petrie*, etc.) can be planted in mixed swards with the legume *Neonotonia wightii* (W.&A.) Verdc. and offer improved pasture management capabilities (Patterson, 1984). Most plants flower March to June, but the dwarf cultivars also flower irregularly throughout the year. (1315)

P. mertensii Roth ex Roemer & Schultes, Syst. Veg. 2: 458. 1817. *P. altissimum* G. Meyer, Prim. Fl. Esseq. 63. 1818. *P. elatior* Kunth, Révis. Gramin. 1: 38. 1829, non L., 1781. *P. megiston* Schultes, Mant. 2: 248. 1824. *P. equisetum* Nees ex Doell in Mart., Fl. Bras. 2(2): 206. 1877, as synonym.

Occasional, an emergent aquatic forming colonies in roadside ditches and along disturbed streamsides under bridges; flowering in February. Distribution: Mexico and the West Indies to Argentina; Bolivia: the Beni. (1745)

P. millegrana Poir. in Lam., Encycl. Suppl. 4: 278. 1816. *P. rugulosum* Trin., Gram. Panic. 195. 1826. *P. lasianthum* Trin., Sp. Gram. 3, pl. 245. 1830. *P. dispersum* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 3: 282. 1835. *P. subglobosum* Hack., Bull. Herb. Boissier, sér. 2, 4(3): 274. 1904.

Similar to and possibly not distinct from *P. sellowii*. Common, seasonal forest, forest/savanna margins, and transitional scrub, forming large colonies in forest openings; palatable (4); flowering November to (*January*, *February*) June. Distribution: Mexico to Argentina. (835, 966, 1489, 1675, 2320)

P. olyroides H.B.K., Nov. Gen. Sp. 1: 102. 1816. *P. probiscidium* Trin., Gram. Panic. 184. 1826. *P. funkianum* Steudel, Syn. Pl. Glumac. 1: 77. 1854.

Common, *cerrado* and in the well-drained, sandy soils of the Andean Piedmont; somewhat palatable (2), coarse but plants lacking in overgrazed savanna; flowering January (March) to May; the panicle forms a tumbleweed at maturity; $2n = 36$. Distribution: Venezuela to Argentina; Bolivia: Andean Piedmont of Santa Cruz. (868, 1257, 1559, 1646, 1769, 1847, **2398**; *Thomas 5567* NY, LPB)

P. pantrichum Hack., Verh. Zool.-Bot. Ges. Wien 195: 72. 1915. *P. protractum* Mez, Notizbl. Bot. Gart. Berlin-Dahlem 7: 77. 1917. *P. warmingii* Mez, Bot. Jahrb. Syst. 56(125): 1. 1921.

Locally abundant in low forest scrub on Serranía San Lorenzo, spreading upslope into margins of *campo rupestre*; rarely in *Orbignya* forests near Santa Rosa de la Roca; flowering November to April. Distribution: Central America to Argentina; Bolivia: the Yungas. (1391, 1972)

P. parviflorum Lam., Tabl. Encycl. 1: 173. 1791. *P. brasiliense* Sprengel, Syst. Veg. 1: 321. 1825.

Common, in seasonally inundated savanna, seasonal ponds, and lake margins; flowering November to (*January*) May. Distribution: throughout the tropics; Bolivia: Andean Piedmont of Santa Cruz and the Beni. (735, 801, 1251, 1254, 1523, 1779, 2278)

P. peladoense Henrard, Blumea 4: 504. 1941. *P. bergii* var. *leiophyllum* Hack. & Lindman, Köngl. Svenska Vetensk. Acad. Handl. 34(6): 10, pl. 4B. 1900. *P. campestre* Nees, Agrost. Bras. 197. 1829, non Nees in Trin., 1826. *P. cayennense* var. *campestris* (Nees) Pilger, Bot. Jahrb. Syst. 30: 132. 1901.

Rare, disturbed ground; more common on margins of savanna/scrub of the Andean Piedmont of Santa Cruz; flowering October to January. Distribution: Brazil to Argentina. (823, 1236)

P. pilosum Sw., Prodr. Veg. Ind. Occ. 22. 1788. *P. distichum* Lam., Encycl. 4: 731. 1798. *Setaria disticha* (Lam.) H.B.K., Nov. Gen. Sp. 1: 112. 1816. *P. pilisparsum* G. Meyer, Prim. Fl. Esseq. 57. 1818. *P. trichophorum* Schrader ex Schultes, Mant. 2: 247. 1824. *P. densiflorum* Willd. ex Spreng., Syst. Veg. 1: 320. 1825. *P. distans* Willd. ex Spreng., Syst. Veg. 1: 305. 1825.

Uncommon, gallery or swamp forest; common as a weed along roads in forest and savanna soils; palatable (5); flowering throughout the year. Distribution: Mexico and the West Indies to Argentina; Bolivia: Beni and the Yungas. (605, 730, 748, 792, 1054, 1515, 1689, 1741, 1880, 1961, 2319)

P. polygonatum Schrader ex Schultes, Mant. 2: 256. 1824. *P. potamium* Trin., Gram. Panic. 239. 1826. *Setaria polygonata* (Schrader) Kunth, Révis. Gramin. 1: 47. 1829. *P. hydrophyllum* Trin. ex Nees, Agrost. Bras. 208. 1829, non Schultes, 1824. *P. pilosum* var. *polygonatum* (Schrader) Doell in Mart., Fl. Bras. 2(2): 211. 1877. *P. ecuadorense* Mez, Bot. Jarhb. Syst. 56(125): 3. 1921.

Rare, humid forest in deep shade; flowering in October. Distribution: Mexico to Paraguay; Bolivia: Andean Piedmont of Santa Cruz and the Yungas. (1380)

P. pulchellum Raddi, Agrost. Bras. 42. 1823. *Eriochloa pulchellum* (Raddi) Kunth, Révis. Gramin. 1: 30. 1829. *P. bipustulatum* Schlect., Linnaea 26: 135. 1853.

Rare, seasonal forest and forest margins; flowering December to May. Distribution: Brazil; Bolivia: the Yungas. (653, 2073)

P. quadriglume (Doell) Hitchc., Contr. U.S. Natl. Herb. 24(8): 460. 1927. *P. cayennense* var. *quadriglume* Doell in Mart., Fl. Bras. 2(2): 220. 1877. *P. bergii* var. *quadriglume* Henrard, Meded. Rijks-Herb. 40: 52. 1921. *P. eccentricos* Hitchc. & Chase ex Rojas, Revista Jard. Bot. Mus. Hist. Nat. Paraguay 2: 164. 1930, nomen nudum.

Common but never abundant, *cerrado*; somewhat palatable (3); flowering January (*March*) to May; $2n = 18$. Distribution: Brazil and Paraguay; Bolivia: Andean Piedmont of Santa Cruz and the Yungas. (736, 758, 856, 891, 1563, 1616, 1770, 1828, 1848, **2397**)

P. rudgei Roemer & Schultes, Syst. Veg. 2: 444. 1817. *P. scoparium* Rudge, Pl. Guian. 1: 21, pl. 29, 1805, non Lam., 1798. *P. pilosissima* Roth ex Roemer & Schultes, Syst. Veg. 2: 458. 1817. *P. dasytrichum* Spreng., Syst.

Veg. 1: 317. 1825. *P. rhigiophyllum* Steudel, Syn. Pl. Glumac. 1: 76. 1854. *P. cayennensis* var. *divaricatum* Doell in Mart., Fl. Bras. 2(2): 220. 1877.

Occasional, weed along roads and as a natural constituent in *campo rupestre*/forest scrub margin on Serranía San Lorenzo; coarse and unpalatable (0); flowering November to March. Distribution: Costa Rica to Brazil; Bolivia: the Yungas. (1397, 1962)

P. scabridum Doell in Mart., Fl. Bras. 2(2): 201. 1877.

Rare, seasonally inundated savanna and forest scrub; flowering November to January. Distribution: the Guianas and Brazil; Bolivia: the Beni. (1514, 1688)

P. schwackeanum Mez, Bot. Jahrb. Syst. 56(125): 1. 1921. *P. helobium* Mez ex Ekman, Ark. Bot. 11: 23. 1921. *P. cyanescens* var. *latifolium* Doell in Mart., Fl. Bras. 2(2): 263. 1877.

Occasional, seasonally inundated savanna; flowering January to March; $2n = 60$. Distribution: Brazil, Paraguay, Uruguay, Argentina. (1634, **2413**)

P. sellowii Nees, Agrost. Bras. 153. 1829. *P. beyrichii* Kunth, Révis. Gramin. 2: 231, pl. 27. 1830. *P. puberulum* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 3: 277. 1835, non Kunth, 1829. *P. probandum* Steudel, Syn. Pl. Glumac. 1: 76. 1854. *P. rugulosum* var. *condensatum* Hack., Feddes Repert. Spec. Nov. Regni Veg. 6: 343. 1909.

Occasional, forest margin and low forest scrub; palatable (5); flowering January to February. Distribution: Mexico and the West Indies to Argentina; Bolivia: Chapare and the Yungas. (831, 1732, 2105)

P. stenodes Griseb., Fl. Brit. W. Ind. 547. 1864. *P. caricoides* var. *glabriusculum* Doell in Mart. Fl. Bras. 2(2): 239. 1877.

Common, seasonally inundated savanna; coarse but somewhat palatable (2) and less common in overgrazed savannas. Flowering is stimulated by fire but plants also bloom irregularly throughout the year. Distribution: Central America and the West Indies to Brazil; Bolivia: the Beni. (610, 710, 1025, 1199, 2075, 2268, 2269, 2770, 2825)

P. stoloniferum Poir. in Lam., Encycl. Suppl. 4: 274. 1816. *P. frondescens* G. Meyer, Prim. Fl. Esseq. 56. 1818. *P. olyrifolium* Raddi, Agrost. Bras. 43. 1823. *P. ctenodes* Trin., Sp. Gram. 2, pl. 171. 1829.

Common, forming colonies in gallery forests or along streams in seasonal forest; palatable (5); flowering November to May. Distribution: Central America and the West Indies to Argentina; Bolivia: Andean Piedmont of Santa Cruz, Beni, and the Yungas. (606, 682, 1386, 1519, 2029)

P. trichanthum Nees, Agrost. Bras. 210. 1829. *P. guayaquilense* Steudel, Syn. Pl. Glumac. 1: 85. 1854.

Common weedy species of forest openings, pastures, and along roads, from deep shade to full sunlight, in well-drained, seasonally inundated or marshy soils; palatable (4); flowering throughout the year. Distribution: Mexico and the West Indies to Paraguay; Bolivia: Chapare and the Yungas. (899, 1053, 1091, 1259, 1556, 1970, 2773)

P. trichoides Sw., Prodr. Veg. Ind. Occ. 24. 1788. *P. capillaceum* Lam., Tabl. Encycl. 1: 173. 1791.

Common weed in forest openings and along well-shaded roads in forest; palatable (4); flowering November to April. Distribution: throughout the tropics. (552, 604, 836, 1892, 1971)

P. tricholaenoides Steudel, Syn. Pl. Glumac. 1: 68. 1854. *P. junceum* Nees, Agrost. Bras. 159. 1829, non Trin., 1826. *P. bambusoides* Speg. ex Arechav., Anales Mus. Nac. Montevideo 1: 128, pl. 9, 10. 1894, non Desv. ex Ham., 1825. *P. pilgeri* Herter, Herb. Corn. Osten. Com. 1: 2. 1925, non Mez, 1904.

Occasional, seasonally inundated savanna; flowering November to *January*. Distribution: Colombia to Argentina; Bolivia: Andean Piedmont of Santa Cruz and the Beni where it is a zonal dominant in seasonally inundated savannas (Beck, 1984). (720, 778, 1505)

Pappophorum Schreb.

Pensiero, J. F. 1986. Revisión de las especies Argentinas del género *Pappophorum* (Gramineae, Eragrostoideae, Pappophoreae). Darwiniana 27: 65–87.

KEY TO SPECIES

1a. Basal lemma of each spikelet inflated, 2–2.5 mm × 1.8–2.5 mm wide (when viewed later-

ally), with 19–26 awns, the second lemma bisexual (rarely sterile) ..... *P. krapovickasii*
1b. Basal lemma of each spikelet thin, 1 1.2 mm × 0.3–1 mm wide, with 11–15 awns, the second lemma sterile ..... *P. pappiferum*

P. krapovickasii Roseng., Comun. Bot. Mus. Hist. Nat. Montevideo IV(58): 1–5. 1975.

Rare, as a weed in disturbed places; flowering November to February. Distribution: Argentina and Paraguay. (1520, 1729)

P. pappiferum (Lam.) Kuntze, Revis. Gen. Pl. 3(2): 365. 1898. *Saccharum pappiferum* Lam., Tabl. Encycl. 1: 155. 1791. *P. alopecuroideum* Vahl., Symb. Bot. Upsal. 3: 10. 1794. *P. laguroideum* Schrader ex Schultes, Mant. 2: 342. 1824. *P. macrostachyum* Schrader ex Schultes, Mant. 2: 342. 1824. *P. elongatum* Sprengel, Syst. Veg. 4(2): 34. 1827. *P. polystachyum* Kunth, Révis. Gramin. 2: 435. 1831. *P. saccharoides* Griseb., Symb. Fl. Arg. 301. 1879.

Rare, as a weed along roads near San Ignacio de Velasco; flowering October to January. Distribution: Mexico to Argentina; Bolivia: Cochabamba, Tarija, and the Gran Chaco. (1308, 1684)

Paspalum L.

Chase, A. 1929. The North American species of *Paspalum*. Contr. U.S. Natl. Herb. 28(1): 1–310. Chase, A. The South American species of *Paspalum*, unpublished manuscript on file at the Hitchcock-Chase Library, U.S. National Herbarium, Smithsonian Institution, Washington, D.C.

KEY TO SPECIES

1a. Spikelets densely pubescent.
  2a. Upper glume glabrous, broadly winged and cordate-based; lower lemma with stiff papillose-based hairs; spikelets 5.5–7 mm long ..... *P. pectinatum*
  2b. Upper glume pubescent, ciliate, or glabrous, neither winged nor cordate-based; lower lemma glabrous or pubescent; spikelets 0.8–5 mm long.
    3a. Racemes 10–20; spikelets softly pilose ..... *P. urvillei*
    3b. Racemes 1–6; spikelets variously pubescent.
      4a. Upper glume with stiff, erect or spreading, submarginal hairs or cilia.
        5a. Rachis foliaceous, 5–9 mm wide; pedicels with a ring of hairs at apex; racemes 1, subtended by a sterile bract inserted at the apex of the peduncle (rarely the bract developed into a second conjugate raceme) ..... *P. stellatum*
        5b. Rachis not foliaceous or only slightly so, less than 3 mm wide; pedicels various; racemes 1–many.
          6a. Spikelets narrowly elliptic, 4–5 mm long; submarginal cilia of the glume well developed on the lower half (2–4 mm long) but lacking or short-ciliate above ..... *P. carinatum*
          6b. Spikelets elliptic to ovate, 2–3.5 mm long; submarginal cilia of the glume well developed on the upper half (2–4 mm long) or along the entire length.
            7a. Racemes 1 5, borne on an elongate axis; spikelets 2–3.5 mm long; upper glume irregularly long-ciliate (1 4 mm) throughout its length, the stouter cilia tuberculate-based, the margins corky ..... *P. polyphyllum*
            7b. Racemes 2, conjugate; spikelets 2 mm long; upper glume long-ciliate towards the apex (1–2 mm), short-ciliate on the lower half (0–0.2 mm), the cilia not tuberculate-based, the margins not corky ..... *P. malmeanum*
      4b. Upper glume uniformly pubescent, lacking stiff submarginal hairs or cilia.
        8a. Raceme solitary; spikelets 1.8–2 mm long, the hairs on upper glume and lower lemma tuberculate-based ..... *P. ekmanianum*
        8b. Racemes 3–6; spikelets 3–5 mm long, the hairs on upper glume and lower lemma not tuberculate-based.
          9a. Leaf blades 8–20 mm wide, flat; spikelets 3.5–5 mm long; lower lemma acute ..... *P. erianthum*
          9b. Leaf blades 2–4 mm wide, involute; spikelets 2.8–3.5 mm long; lower lemma blunt ..... *P. ammodes*
1b. Spikelets not densely pubescent –either glabrous, puberulent, or minutely ciliate.
  10a. Upper glume (as well as the lower glume) lacking or reduced to a membranous scale, the back of the upper lemma exposed.
    11a. Upper lemma prominently 3–5-nerved ..... *P. malacophyllum*
    11b. Upper lemma nerveless or the nerves indistinct.
      12a. Apex of pedicel bearded; upper glume lacking ..... *P. gardnerianum*
      12b. Apex of pedicel glabrous; upper glume a membranous scale covering ¼ of upper floret ..... *P. inaequivalve*

10b. Upper glume well developed, equal or subequal to spikelet.
13a. Spikelets 1–2 mm long.
14a. Upper floret dark chestnut brown ..... section *Plicatula*, go to lead 28b
14b. Upper floret stramineous.
15a. The margins of the glume ciliate, the spikelets suborbicular, acute ..... *P. conjugatum*
15b. The glume glabrous or puberulent but not ciliate, the spikelet orbicular, elliptic, or obovate.
16a. Racemes 6–15(20); caespitose perennials.
17a. Racemes stiffly ascending, the rachis ciliate, 1–5 cm long; foliage succulent, the blades 2–4 mm wide, stiffly ascending ..... *P. humigenum*
17b. Racemes lax, the rachis glabrous, 3–10 cm long; foliage not succulent, the blades 5–15 mm wide, lax ..... *P. paniculatum*
16b. Racemes 1–3(4); caespitose annuals or perennials.
18a. Upper glume and lower lemma with glandular hairs or globular, glassy papillae; annuals.
19a. Spikelets 0.8 mm long; pedicels flattened, erect; racemes 2–3, borne on a short axis ..... *P. parviflorum*
19b. Spikelets 1–1.8 mm long; pedicels terete or triquetrous; racemes 1 or 2, if 2 then conjugate (rarely a third below).
20a. Spikelets orbicular, the upper glume and lower lemma provided with globular, glassy papillae ..... *P. multicaule*
20b. Spikelets obovate to elliptic, the upper glume and lower lemma provided with glandular-tipped hairs .... *P. clavuliferum*
18b. Upper glume and lower lemma glabrous; annuals or perennials.
21a. Upper floret rugose; upper glume and lower lemma not covering the sides of the upper floret; spikelets obovate; annual .... *P. pictum*
21b. Upper floret smooth; upper glume and lower lemma covering the sides of the upper floret; spikelets elliptic; perennial ..... *P. pumilum*
13b. Spikelets 2–4 mm long.
22a. Racemes 2, conjugate or nearly so (rarely a third raceme below).
23a. Spikelets mottled with purple (brown in old or alcohol specimens), 2.2–2.5 mm long, broadly elliptic, blunt ..... *P. maculosum*
23b. Spikelets not mottled, 2.2–5 mm long, narrowly elliptic to orbicular, acute to blunt.
24a. Racemes reflexed at maturity; plants stoloniferous perennials of sandy soils ..... *P. vaginatum*
24b. Racemes ascending at maturity; plants caespitose, stoloniferous or rhizomatous perennials.
25a. Spikelets narrowly elliptic, 3 times as long as wide; plants caespitose, not a turf grass.
26a. Spikelets 1.5–2 mm wide; racemes subconjugate or conjugate, pilose at base ..... *P. lineare*
26b. Spikelets 1 mm wide; racemes strictly conjugate, glabrous at base ..... *P. pallens*
25b. Spikelets ovate to suborbicular; rhizomatous turf grasses.
27a. Spikelets 2.5–2.8 mm long, orbicular, blunt ..... *P. minus*
27b. Spikelets 3–4 mm long, broadly elliptic, acute ..... *P. notatum*
22b. Racemes 1–many, borne on a short to elongate axis, neither conjugate nor subconjugate.
28a. Rachis 1–3 mm wide, flattened or foliaceous; upper florets slightly convex, stramineous, tan, or dark brown.
29a. Rachis 2–3 mm wide; plants decumbent and rooting at the nodes.
30a. Rachis 3 mm wide; spikelets acuminate; upper floret stramineous; culms prostrate or scandent ..... *P. acuminatum*
30b. Rachis 2 mm wide; spikelets blunt; upper floret stramineous, tawny or dark brown, when dark brown then the margins of the upper lemma white; culms erect ..... *P. wrightii*
29b. Rachis about 1 mm wide, flattened; plants caespitose perennials.
31a. Racemes more than 40; basal sheaths strongly equitant, succulent, and with reticulate venation.
32a. Spikelets elliptic; axis of inflorescence (20)30–50 cm long ..... *P. intermedium*
32b. Spikelets suborbicular; axis of inflorescence 15–20(25) cm long ..... *P. densum*
31b. Racemes 4–15; basal sheaths compressed to rounded but not strongly equitant, lacking reticulate venation.
33a. Racemes 1–3 cm long, arcuate, ascending; upper florets stramineous; leaf blades lacking serrated margins ..... *P. lividum*

33b. Racemes 5–15 cm long, laxly ascending; upper florets cream-colored to dark brown; leaf blades with serrated (cutting) margins.
34a. Spikelets 2.5–3.2 mm long, strongly obovate; upper glume and lower lemma green or brown, not purple spotted, the upper glume pubescent near the apex; upper floret very dark brown ..... *P. virgatum*
34b. Spikelets 2.2–2.5 mm long, elliptic to obovate; upper glume and lower lemma purple spotted, glabrous; upper floret cream-colored to dark brown ..... *P. conspersum*

28b. Rachis 0.5 mm wide, triquetrous or terete; upper florets strongly plano-convex; dark brown and shiny (sect. *Plicatula*).
35a. Spikelets 1.8 3 mm long.
36a. Lower lemma indurate, dark brown and shining, similar to the upper floret; spikelets biconvex (i.e., both upper and lower florets plano-convex) ..... *P. lenticulare* f. *intumescens*
36b. Lower lemma not indurate, bicolored (the margins light tan and thickened, surrounding a dark brown, papery center); spikelets plano-convex.
37a. Spikelets 2–3 mm long; lower lemma plicate, with transverse wrinkles spreading inward from the thickened margins.
38a. Spikelets 2–2.5 mm long, elliptic; blades folded, the sheaths compressed; plants of savanna wetlands ..... *P. lenticulare*
38b. Spikelets 2.5–3.0 mm long, broadly elliptic to obovate; blades flat, the sheaths somewhat compressed or rounded on the back; plants of well-drained soils ..... *P. plicatulum*
37b. Spikelets 1.8–2 mm long; lower lemma not plicate, lacking transverse wrinkles ..... *P. limbatum*
35b. Spikelets 3–4 mm long.
39a. Upper glume and lower lemma with irregular reticulate wrinkles, generally glaucous between the wrinkles ..... *P. gemniflorum*
39b. Upper glume and lower lemma either lacking reticulate wrinkles, or with transverse wrinkles (plicate) on the lower lemma only.
40a. Culms stout, about 5 mm in diameter; racemes 10–20; spikelets elliptic ..... *P. atratum*
40b. Culms 1–3(5) mm in diameter; racemes 2–6; spikelets obovate or broadly elliptic.
41a. Lower lemma bicolored, with transverse wrinkles spreading inward from the thickened margins (plicate); axils of racemes pilose ..... *P. guenoarum*
41b. Lower lemma not bicolored, the margins similar to the central area, lacking transverse wrinkles; axils of racemes glabrous or sparsely pilose.
42a. Spikelets 3–3.4 mm long, glabrous at base of bracts; lower glume absent; axils of racemes glabrous ..... *P. macedoi*
42b. Spikelets 3.7–3.9 mm long, minutely pubescent at the base along the line of the insertion of the glumes and the lower lemma; lower glume present, vestigial or a narrow triangular bract ¼ the length of to subequaling the spikelet; axils of racemes sparsely pilose ..... *P. kempffii*

P. acuminatum Raddi, Agrost. Bras. 25. 1823.

Rare, as a floating aquatic in artificial pond. Distribution: United States to Argentina; Bolivia: the Beni. (2325)

P. ammodes Trin., Gram. Panic. 120. 1826. *P. sordidum* Hack., Oesterr. Bot. Z. 51: 197. 1901.

Locally common in *cerrado* and *campo rupestre* near Santiago de Chiquitos; flowering is dependent on fire. Distribution: northern South America to Brazil and Paraguay. (2781, 2786)

P. carinatum Humb. & Bonpl. ex Flügge, Gram. Monogr., *Paspalum* 65. 1810. *P. kappleri* Hochst. in Steudel, Syn. Pl. Glumac. 1: 21. 1854. *P. stellatum* sensu Trin., Sp. Gram. 1: 119. 1828.

Occasional, seasonally humid savannas with sandy soils near Santa Rosa de la Roca (Prva. Velasco); flowering October to January, apparently stimulated by fire. Distribution: northern South America to Brazil. (1436, 1659, 2823)

P. clavuliferum Wright, Anales Acad. Cienc. Habana 8: 203. 1871. *P. falcula* Doell in

Mart., Fl. Bras. 2(2): 61. 1877. *P. horticola* Salzm. ex Doell in Mart., Fl. Bras. 2(2): 61. 1877, as synonym. *P. pittieri* Hack. ex Beal, Gr. of N. Amer. 2: 88. 1896.

Uncommon, in seasonal pools or humid sandy soils on granitic outcrops; flowering November to January. Distribution: Mexico and the West Indies to Brazil. (811, 1534)

P. conjugatum Bergius, Act. Helv. Phys. Math. 7: 129, t. 8. 1762. *P. renggeri* Steudel, Syn. Pl. Glumac. 17. 1854.

Common, as a weed in pastures and along paths and roadsides in forest; palatable (4); flowering December to (*January*) April. Distribution: throughout the tropics. (650, 673, 749, 814, 1679, 1752)

P. conspersum Schrader ex Schultes, Mant. 2: 174. 1824.

Common, seasonally inundated savanna; palatable (2); flowering October to (*January*) February; $2n$ = about 40, abnormal meiosis indicates the species is probably apomictic. Distribution: Mexico to Argentina; Bolivia: the Yungas. (845, 1632, **2317**)

P. densum Poir. in Lam., Encycl. 5: 32. 1804. *P. paniceum* Smith in Rees, Cycl. 26: 14. 1813.

Rare, roadside ditch in seasonally inundated soils; flowering in January. Distribution: Central America and the West Indies to Brazil; Bolivia: Andean Piedmont of Santa Cruz and the Beni. (2301)

P. ekmanianum Henrard, Meded. Rijks-Herb. 40: 49. 1921.

This species is similar to *P. verrucosum* Henrard of Paraguay and southern Brazil, which has more distantly placed spikelets 2.6–3.2 mm long and a zigzag rachis (vs. spikelets 1.8–2.2 mm long and a straight rachis in *P. ekmanianum*). Rare in Chiquitanía where it is restricted to sandy, superficial soils on Serranía de San Lorenzo (*campo rupestre*), more common on the Andean Piedmont and the montane tropical savannas near Samaipata; flowering April to June. Distribution: apparently a Bolivian endemic. (1980, 2491)

P. erianthum Nees ex Trin., Gram. Panic. 121. 1826.

Common, in *cerrado* and *campo rupestre*. Somewhat palatable (2), although the foliage is coarse, the relative abundance of this species is markedly decreased in overgrazed savannas. Individual plants are variable within populations for foliage vestiture, inflorescence morphology, and spikelet size; all populations sampled near Concepción exhibited an abnormal meiosis indicating that the species is probably apomictic; flowering is dependent upon fire. Distribution: Central America, Brazil, and Paraguay; Bolivia: Andean Piedmont of Santa Cruz. (1139, 1194, 1369, 2191, 2779)

P. gardnerianum Nees, Hooker's J. Bot. Kew Gard. Misc. 2: 103. 1850. *P. gardnerianum* var. *oligostachyum* Doell in Mart., Fl. Bras. 2(2): 42. 1877. *P. gardnerianum* var. *vestitum* Kuhlm., Comiss. Linhas Telegr. Estratég. Mato Grosso Amazonas 67, Annexo 5, 11: 49. 1922.

Locally abundant on Serranía de San Lorenzo (*campo rupestre*), possibly present on other serranias but overlooked due to lack of flowering populations at time of visits; flowering in April. Distribution: northern South America to Argentina. (1396, 1984)

P. humigenum Swallen, Phytologia 14: 362. 1966. *P. denticulatum* var. *ciliatum* Trin., Sp. Gram. 123. 1829.

Common to abundant in seasonal ponds and inundated savannas; palatable (4); flowering November to (*December*) January; $2n$ = 20. Distribution: Venezuela and Brazil. (702, 708, 1655, **2246**; *Bruderreck 113* ISC, LPB)

P. inaequivalve Raddi, Agrost. Bras. 28. 1823. *P. inaequivalve* var. *glabriflorum* Hack. ex Stuck., Anales Mus. Nac. Hist. Nat. Buenos Aires 21: 23. 1911. *P. glabriflorum* (Hack.) Herter, Revista Sudamer. Bot. 6: 138. 1940.

Uncommon, forest floor in deep shade and forest/savanna margins; flowering February to May. Distribution: Brazil, Uruguay, and Argentina; Bolivia: Beni and the Yungas. (870, 1753, 2028)

P. intermedium Munro ex Morong, Ann. N.Y. Acad. Sci. 7: 258. 1893.

Very similar and possibly not distinct from *P. plenum* Chase and *P. turriforme* R. W. Pohl of Central and northern South America. Abundant in savanna marsh and seasonally inundated savanna; flowering November (*December*) to February; abnormal meiosis indicates the species is probably apomictic. Distribution: Brazil, Paraguay, Uruguay, and Argentina. (1631, 1673, 2258)

P. lineare Trin., Gram. Panic. 99. 1826. *P. angustifolium* Nees, Agrost. Bras. 64. 1829, non Leconte, 1820 nec Nees ex Trin., 1826. *P. neesii* Kunth, Révis. Gramin. 1: 25. 1829. *P. tropicum* Doell in Mart., Fl. Bras. 2(2): 83. 1877. *P. furcellatum* S. Moore, Trans. Linn. Soc. London, Bot. 2(4): 505, pl. 34. 1895.

Plants are variable among populations for spikelet size and the presence of a third subdigitate raceme. This species is zonally abundant in sandy soils of valley-side *campos* (upslope) and seasonally humid savanna; it is less common in seasonally inundated savanna and savanna marsh; coarse and unpalatable (0). Flowering is dependent upon fire; abnormal meiosis indicates the species is probably apomictic. Distribution: Mexico and the West Indies to northern Argentina; Bolivia: the Beni. (783, 1160, 1324, 1366, 1803, 2218, 2772)

P. lividum Trin. in Schlect., Linnaea 26: 383. 1854. *P. proliferum* Arechav., Anales Mus. Nac. Montevideo 1: 52. 1894. *P. hieronymii* Hack., Oesterr. Bot. Z. 51: 198. 1901.

Rare, seasonal pond. Distribution: Mexico to Argentina. (1719)

P. maculosum Trin., Gram. Panic. 98. 1826. *Paspalum notatum* var. *maculatum* Nees, Hooker's J. Bot. Kew Gard. Misc. 2: 104. 1850.

Occasional, seasonally humid savanna and valley-side *campos*; palatable (4); flowering from *January* to April; $2n = 40$. Distribution: northern South America to Uruguay and Argentina. (1640, 1645, 1959, **2282**)

P. malacophyllum Trin., Sp. Gram. 3: pl. 271. 1831. *Anachyris paspaloides* Nees, Hooker's J. Bot. Kew Gard. Misc. 2: 103. 1850.

This species is part of the *Anachyris* group, an extremely variable taxon with several intergrading forms. Burkhart (1969) recognized three species *P. malacophyllum* with leaf blades 1–3 cm wide, *P. simplex* Morong with leaf blades 2–5 mm wide, and *P. elongatum* Griseb. with pilose rachis margins. In Chiquitanía the morphology ranges from plants with stout culms, leaf blades 3 cm wide, and large panicles with more than 50 racemes each 10–13 cm long to delicate plants (rarely scandent) with leaf blades about 5 mm wide and panicles with 4–5 racemes, each 2–6 cm long; spikelet size varies independently, ranging from 1.5 to 2.5 mm long. Significantly, life form is not strictly correlated with habitat and wide-bladed plants can occur in relatively full sunlight (*Killeen 1855*), while narrow-bladed plants can occur underneath a closed canopy (*Killeen 1845*). The entire group is in need of a careful systematic revision. Common, restricted to forest/*cerrado* margins and low scrub; palatable (3); flowering January to (*March*) April; $2n = 40$. Distribution: northern South America to Paraguay; Bolivia: Cochabamba and the Yungas. (1095, 1722, 1727, 1845, 1855, **1918,** 1974, 2330, 2449)

P. malmeanum Ekman, Ark. Bot. 10(17): 12, pl. 4. 1911.

Rare in herbaria but zonally abundant on valley-side *campos* (midslope); foliage coarse and unpalatable (0); flowering *April* to May; $2n = 20$. Distribution: central Brazil. (898, 2024, 2076, **2478**)

P. minus Fourn., Mex. Pl. 2: 6. 1886.

Rare, forming colonies in disturbed, seasonally humid soils; palatable (4); flowering November to January. Distribution: Mexico to Paraguay; Bolivia: the Yungas. (1521, 1584)

P. multicaule Poir. in Lam., Encycl. Suppl. 4: 309. 1816. *P. papillosum* Sprengel, Novi Provent. 47. 1819.

Common, in seasonally humid sandy soils at top of valley-side *campos* and superficial soils (or small ephemeral ponds) on granitic outcrops; flowering September to May. Distribution: Mexico and the West Indies to Brazil; Bolivia: the Yungas. (796, 903, 1218, 1250, 1535, 1540, 1644, 2025)

P. notatum Flügge, Gram. Monogr., *Paspalum* 106. 1810. *P. distachyon* Willd. ex Doell in Mart., Fl. Bras. 2(2): 73. 1877. *P. uruguayense* Arechav., Anales Mus. Nac. Montevideo 1: 53. 1894.

The traditional cultivated forage grass of lowland Bolivia; adapted to forest and savanna soils, this species is highly resistant to overgrazing and soil compaction. Although newly introduced exotic species are more productive and offer better-quality forage, this species is still favored for pastures near the ranch house and as a lawn in parks, yards, and football (soccer) fields; occasionally naturalized in humid sandy soils of valley-side *campos*. Populations flower November to (*January*) February; lo-

cal name: *grama negra*. Distribution: Mexico to Argentina. (594, 1637)

P. pallens Swallen, Phytologia 14: 365. 1966.

Common, forming dispersed colonies in seasonal ponds and seasonally inundated savanna; palatable (4); flowering November (*January*) to May; $2n = 20$. Distribution: central Brazil. (703, 802, 826, 944, 1421, 1464, 1500, 1532, 1590, **2284**)

P. paniculatum L., Syst. Nat. 10(2): 855. 1759. *P. hemisphericum* Poir., Encycl. 5: 31. 1804. *P. compressicaulis* Raddi, Agrost. Bras. 29. 1823. *P. supinum* Rupr. ex Galeotti, Bull. Acad. Roy. Sci. Bruxelles. 9: 237. 1842. *P. affine* Bello, Anales Soc. Esp. Hist. Nat. 12: 125. 1883.

Abundant, as a weed of pastures and roadsides in forest soils; flowering October to June. Distribution: throughout the tropics. (599, 601, 658, 659, 660, 696, 744, 972)

P. parviflorum Rhodé ex Flügge, Gram. Monogr., *Paspalum* 98. 1810. *P. vestitum* Steudel, Syn. Pl. Glumac. 1: 17. 1854, nomen nudum. *P. parviflorum* var. *humilis* Nees, Doell in Mart. 2(2): 45. 1877.

Rare, in seasonal pool on granitic outcrop; flowering in November. Distribution: Central America and the West Indies to Brazil. (1537)

P. pectinatum Nees ex Trin., Sp. Gram. 1: 117. 1828. *Anastrophus pectinatus* (Nees ex Trin.) Schlecht. ex B. D. Jacks., Index Kew. 1: 1, 118. 1893.

Abundant in *campo rupestre* (Serranía de San Lorenzo and Serranía de Santiago); flowering is dependent upon fire. Distribution: Mexico to southern Brazil; Bolivia: the Beni. (2782A, 2833)

P. pictum Ekman, Ark. Bot. 10(17): 11. 1911. *P. maculatum* Nash, N. Amer. Fl. 17: 186. 1912.

Common, seasonally inundated savanna; flowering November to May. Distribution: Central America to Brazil; Bolivia: Andean Piedmont of Santa Cruz. (810, 945, 1490, 1945, 2087, 2454; *Bruderreck 261* ISC, LPB)

P. polyphyllum Nees ex Trin., Gram. Panic. 114. 1826. *P. blepharophorum* sensu Trin., Sp. Gram. 2(11): pl. 134. 1829. *P. distichophyllum* sensu Doell in Mart., Fl. Bras. 2(2): 65. 1871. *P. macroblepharum* Hack., Oesterr. Bot. Z. 51: 196. 1901. *P. biciliatum* Mez, Feddes Repert. Spec. Nov. Regni Veg. 15: 27. 1917.

This species has two variants: sparsely branched, large-leaved plants that grow in relatively well-developed soils and freely branched, small-leaved plants that are rooted in the cracks of granitic outcrops and boulders. The Andean species *P. humboldtianum* Flügge exhibits a similar phenomenon but is distinguished from *P. polyphyllum* by the presence of uniform, lashlike cilia on the upper glume rather than having cilia of irregular length interspersed with stout trichomes. Uncommon, in *campo rupestre* (Serranía de San Lorenzo and Serranía de Santiago); only senescent specimens have been collected (October), probably flowering late in the rainy season (May). Distribution: Brazil, Paraguay, Uruguay, and Argentina; Bolivia: Andean Piedmont and montane tropical grasslands near Samaipata, Santa Cruz. (1398, 2795; *Cutler 7019* US)

P. pumilum Nees, Agrost. Bras. 52. 1829. *P. campestre* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 3: 144. 1835. *P. bicrurulum* Salzm. ex Steudel, Syn. Pl. Glumac. 1: 21. 1854.

Rare, ephemeral ponds of granitic outcrops; flowering in November. Distribution: the West Indies to Uruguay and Argentina. (2335)

P. stellatum Humb. & Bonpl. ex Flügge, Gram. Monogr., *Paspalum* 62. 1810. *P. stellatum* var. *monostachyum* Nees, Agrost. Bras. 78. 1829. *P. stellatum* var. *distachyum* Nees, Agrost. Bras. 78. 1829. *P. cujabense* Trin., Sp. Gram. 3: pl. 284. 1831. *P. wagnerianum* Schlect., Linnaea 26: 133. 1853. *P. splendens* var. *sphacelatum* Hack., Oesterr. Bot. Z. 51: 239. 1901. *P. stellatum* f. *hirsuta* Hack. in Stuck., Anales Mus. Nac. Hist. Nat. Buenos Aires 21: 28. 1911.

Two variants of this species exist in Chiquitanía with distinctive morphologies, chromosome numbers, and habitat preferences. The more common genotype (*P. cujabense*) has deep purple rachis wings, spikelets 2 mm long, and a chromosome number of $2n = 20$ (*Killeen 2487*); it is found as a dominant in a zonal sequence on valley-side *campos* (upslope) and in seasonally humid savannas. Less common in herbaria but locally abundant

around Concepción is a more robust genotype (*P. stellatum* var. *monostachyum*) with golden brown rachis wings, spikelets 3 mm long, and a chromosome number of $2n = 32$ with normal meiosis (*Killeen 2477*); this is restricted to well-drained *cerrado* and frequently forms distinct colonies in association with lateritic crests. The US type fragment (*Humboldt & Bonpland s.n.*) of this species (sensu lato) has spikelets intermediate to the two genotypes and the traditional circumscription of the species is maintained. Both variants appear to be somewhat palatable (2). Different populations flower asynchronously in *March*, *April*, and May; several dozen inflorescences of both genotypes were scored for seed set, but none produced seed. Distribution: Mexico and the West Indies to Argentina; Bolivia: Andean Piedmont of Santa Cruz. (687, 904, 1952, 1998, 2011B, 2458, 2473, 2474, **2477, 2487**)

P. urvillei Steudel, Syn. Pl. Glumac. 1: 24. 1854. *P. ovatum* var. *parviflorum* Nees, Agrost. Bras. 43. 1829. *P. larranagae* Arechav., Anales Mus. Nac. Montevideo 1: 60. 1894. *P. dilatatum* var. *parviflorum* Doell in Mart., Fl. Bras. 2(2): 64. 1877.

Not yet collected in Chiquitanía. Rare, as a weed in roadside ditches of the Andean Piedmont but more common in the irrigation ditches of the intermontane valleys of the Andes. Distribution: United States to Argentina. (2121, 2508)

P. vaginatum Sw., Prodr. 21. 1788. *P. vaginatum* var. *longipes* Lange, Vidensk. Meddel. Dansk. Naturhist. Foren. Kjobenhavn 1854: 44. 1855.

Seasonal pond with sandy soils. Distribution: throughout the tropics. (1574)

P. virgatum L., Syst. Nat. ed. 10. 2: 855. 1759.

Common, as a weed in disturbed marshes, streamsides, and roadside ditches; flowering October to February; local name: *cortadera*. Distribution: southern United States to Argentina; Bolivia: Andean Piedmont of Santa Cruz, Tarija, Beni, and the Yungas. (585, 716, 1317, 1503; putative hybrids with *P. plicatulum* s.l.: 1720, 1721)

P. wrightii Hitchc. & Chase, Contr. U.S. Natl. Herb. 18: 310. September 1, 1917. *P. virgatum* var. *platyaxis* Doell in Mart., Fl. Bras. 2(2): 89. 1877. *P. virgatum* var. *glabriusculum* Doell in Mart., Fl. Bras. 2(2): 89. 1877. *P. plicatulum* var. *multinode* Hack., Feddes Repert. Spec. Nov. Regni Veg. 6: 342. 1909. *P. platyaxis* (Doell) Mez, Feddes Repert. Spec. Nov. Regni Veg. 15: 73. December 31, 1917. *P. texanum* Swallen, Proc. Biol. Soc. Wash. 55: 94. 1942. *P. luticolum* Swallen, Phytologia 14(6): 373. 1967.

Specimens differ in foliage morphology (blades 2 mm wide and involute to 10 mm wide and planate) and the degree of pigmentation of the upper floret (tawny to dark chestnut brown); apparently allied to sect. *Plicatula*, *P. wrightii* is closely related to *P. hydrophyllum* Henrard, which has larger spikelets (2.5–3 mm). Rare, in seasonally inundated savanna and along streambanks; flowering January to March. Distribution: southern United States to Argentina. (764, 1883)

Paspalum sect. **Plicatula**

An extremely variable species complex with numerous intergrading taxa and a center of diversity in south-central Brazil. Populations with identical morphology and phenology are usually restricted to a narrowly defined habitat and/or local geographic area. Most plants sampled in Chiquitanía had abnormal meiosis and disfunctional pollen development (10–70% not staining in analine blue); nonetheless, plants consistently produced viable caryopses at low levels of fertility (10–30% of total florets). Infrequent hybridization followed by apomixis is probably responsible for the origination and maintenance of the genetic diversity in this difficult group. Populations differ in stature, foliage morphology (vestiture, length/width ratios, and the compression of the sheath and blade), inflorescence morphology (number, length, and arrangement of racemes), spikelet size (1.5–4.0 mm long), spikelet shape (narrowly elliptic, obovate, orbicular), and the form of the lower lemma (margins thickened or not, plicate wrinkles present or not, bicolored or concolorous). Numerous species and varieties have been described; most modern floristic treatments have recognized certain distinctive and/or well-collected genotypes, while uniting other forms under *P. plicatulum*. In Chiquitanía, there is a clear correlation between morphology and habitat: populations with conduplicate foliage and small (1.8–2.5 mm long) elliptic spikelets are common in savanna wetland habitats, while populations with planate foliage and larger (2.5–4.0 mm long) widely elliptic to obovate spikelets are common in well-drained *cerrado*. There are exceptions, particularly in central Brazil (e.g., *P. ramosum* Swallen, which

has conduplicate foliage and spikelets 3.2 mm long, is known to occur in humid soils). The following treatment is provisional.

P. atratum Swallen, Phytologia 14(6): 378. 1966. *P. plicatulum* var. *robustum* Hack., Bull. Herb. Boissier, sér. 2 4(3): 269. 1904.

Rare, as a weed in pasture and disturbed places; flowering February to March. Distribution: central Brazil. (1846)

P. gemniflorum Steudel, Syn. Pl. Glumac. 1: 25. 1854. *P. plicatulum* var. *oligostachyum* Doell in Mart., Fl. Bras. 2(2): 77. 1877. *P. reticulatum* Hack., Oester. Bot. Z. 51: 199. 1901.

As in other taxa within sect. *Plicatula*, populations are variable for a number of characters, notably inflorescence morphology and spikelet size; a similar taxon, *P. plicatulum* var. *leptogluma* Pilger, has suborbicular spikelets 2–2.2 mm long. Occasional to locally abundant in *cerrado*; palatable (4); flowering December (*January*) to May. Distribution: northern South America to southern Brazil. (656, 706, 715, 733, 739, 867A, 876, 893, 1618, 1866, 1875, 1877, 1956, 2015, 2443, 2451)

P. guenoarum Arechav., Anales Mus. Nat. Montevideo 1: 50. 1894. *P. guenoarum* var. *vestitum* Henrard, Feddes Repert. Spec. Nov. Regni Veg. 18: 240. 1922. *P. plicatulum* var. *guenoarum* (Arechav.) Roseng., Arrill. & Izag., Gram. Urug. 373. 1970.

Occasional in *cerrado*, particularly on lateritic crests; palatable (4); flowering December to (*February*) March. Distribution: Brazil, Paraguay, Uruguay, and Argentina. (878, 2394)

P. kempffii, Killeen, sp. nov. TYPE: Bolivia. Santa Cruz: Estancia La Pachanga, 5 km S of Concepción, Prva. Ñuflo de Chávez, 16°08′S, 62°05′W, 500 m, *Killeen 2272* (holotype, ISC; isotypes, LPB, F, MO, US, SI, CTE, SP, NY). Figure 5.

P. macedoi Swallen, affinis sed 2–3 racemis, 7–13 cm longis, expansis pedicellis ad apices barbatis a pilis tenuibus 0.2–0.4 mm longis; spiculis 3.6–3.9 mm longis, 2.4–2.7 mm latis, ovatis vel late ellipticis; glumis infernis vestigialibus vel bracteatis anguste triangulariter, 2.5 mm longis, evolutis in dimidiis spicularum; flosculis superis ringentibus, marginalibus lemmatum albis notabilis.

Caespitose perennial from extravaginal innovations; culms erect, 1.2–1.5 m tall; internodes 3–4 mm in diameter, glabrous, ridged, hollow; nodes 3–5 per culm, bearded, the hairs 3 mm long, stiffly ascending. Foliage mainly basal, with the blades reduced above and lacking at the ultimate node; sheaths glabrous, longer than the internodes below, shorter above, keeled, the margins membranous, auriculate; ligules 2.5 mm long, membranous, adnate to the auricle of the sheath; with a wedge-shaped thickening on the abaxial surface between the sheath and the blade; blades 30 cm long at base, 4–6 mm wide, flat or folded, glabrous on the adaxial surface, glaucous on the abaxial surface, the margins smooth, somewhat narrowed at the base, the apex long-acuminate. Inflorescence a panicle of 2–3 racemes placed 5–6 cm apart on a sulcate, glabrous axis; racemes 7–13 cm long, sparsely pilose in the axils, the hairs 5 mm long, stiff; rachis flattened, 1 mm wide, zigzag, bearing spikelets to the tip; pedicels 0.5–1 mm long. Spikelets paired, 3.6–3.8 mm long, 2.5 mm wide, broadly elliptic, strongly plano-convex, disarticulating below the glumes, the back of the upper lemma oriented towards the rachis; a pair of spikelets overlapping the proximal pair by ⅓–½ of their length; a delicate ring of hairs 0.2–0.4 mm long inserted at the base of the bracts. Lower glume lacking, vestigial, or a well-developed, triangular bract 2.5 mm long, distinctly 3-nerved, more regularly developed on the interior spikelet of each pair; upper glume convex, 5–7-nerved, chartaceous, the lateral nerves submarginal, subequaling the upper floret but not covering the apex nor the sides of the upper lemma; lower lemma flat, 7-nerved, the lateral nerves submarginal, chartaceous, green, not bicolored nor with plicate, transverse wrinkles along the unthickened margins; lower palea lacking. Upper floret gaping prior to and after anthesis; upper lemma 3.3–3.6 mm long, broadly elliptic to subglobose, convex, 1.5 mm wide, the apex rounded, dark chestnut brown, cartilaginous, longitudinally striate, the margins white, inrolled, clasping the palea below but not at the apex; upper palea 3–3.3 mm long, subglobose, similar in texture to the upper lemma, with paired lobes at the base enclosing the floral parts. Lodicules 2, truncate, fleshy, 0.8 mm long; anthers 3, 2 mm long, orange; style branches 2, naked and translucent, 0.5 mm long; stigmas plumose, purple, 1.5 mm long, exserted; spikelets chasmogamous.

Locally abundant in *campo cerrado*, particularly over lateritic crests; palatable (3). In addition to several morphological characters, notably the

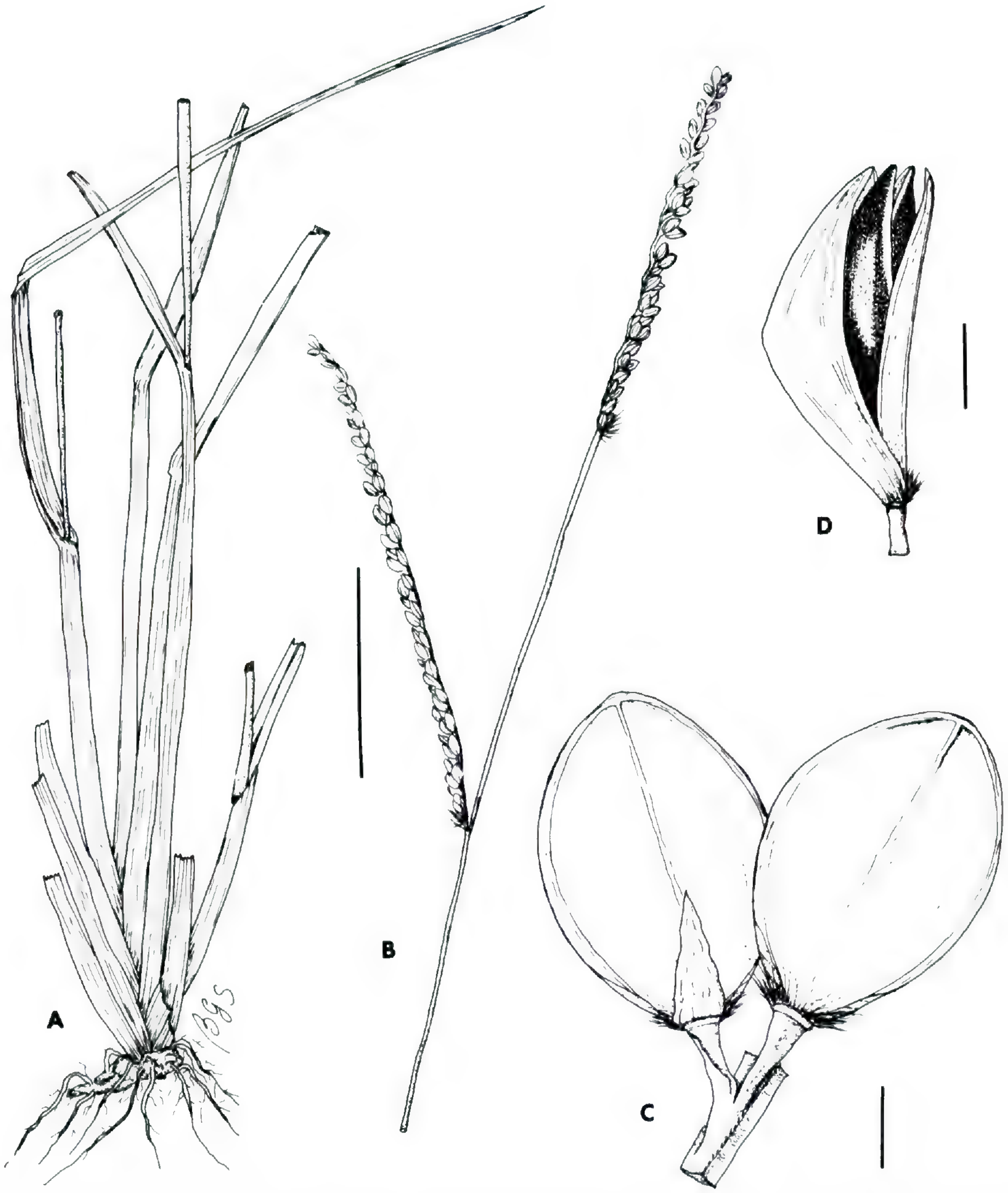

FIGURE 5. *Paspalum kempffii* (*Killeen 2272*).—A. Habit.—B. Inflorescence (A and B: bar = 5 cm).—C. Ventral view of spikelet pair.—D. Lateral view of spikelet (C and D: bar = 1 mm).

distinctly larger spikelets, this segregate species of the *Plicatula* group differs from similar taxa found in well-drained *cerrado* soils (i.e., *P. plicatulum* s.s., *P. guenoarum*, and *P. macedoi*) by flowering earlier in the rainy season, from December to *January*. An abnormal meiosis ($2n$ = about 28, 3 plants sampled), a high proportion of nonstained pollen grains (57%, 8 plants sampled), and low but consistent levels of seed set (14% of total florets, 13 plants sampled) indicates the species is apomictic.

P. lenticulare H.B.K., Nov. Gen. Sp. 1: 92. 1816. *P. atrocarpum* Steudel, Syn. Pl. Glumac. 1: 25. 1854. *P. humile* Steudel, Syn. Pl. Glumac. 1: 25. 1854. *P. compressifolium* Swallen, Phytologia 14(6): 381. 1967. *P. paludosum* Swallen, Phytologia 14(6): 379. 1967. *P. pontanalis* Swallen, Phytologia 14(6): 376. 1967. *P. formosum* Swallen, Phytologia 14(6): 379. 1967.

Common to locally abundant in seasonally inundated and humid savannas, less common in valley-side *campos* and very rarely in *cerrado*; flowering September to (*January*, *February*, *March*) June, individual populations with distinct phenologies. Distribution: Central America to Argentina. (698B, 699, 707, 765, 771, 789, 822, 842, 858, 865, 1231, 1232, 1492, 1498, 1527, 1557,

1561, 1601, 1765, 1838, 1862, 1874, 1882, 2001, 2111, 2112, 2270, 2279, 2291, 2322, 2396, 2417)

P. lenticulare f. **intumescens** (Doell) Killeen, comb. & stat. nov. BASIONYM: *P. plicatulum* var. *intumescens* Doell in Mart., Fl. Bras. 2(2): 78. 1877.

Although forming distinct populations, the foliage, inflorescence morphology, and spikelet size are similar to that of *P. lenticulare*, and a similar phenomenon of an indurated lower lemma occurs in the related plicatuloid species of *P. convexum* Humb. & Bonpl. ex Willd. and *P. foveolatum* Steudel. In Chiquitanía, indurated lower lemmas rarely occur in large-spikelet genotypes as well. Locally abundant at Santa Rosa de la Roca in seasonally humid and shallowly inundated savanna; flowering November to (*January*) February. (761, 763, 803, 844, 1526, 1667, 1670, 1671, 1723)

P. limbatum Henrard, Blumea 4: 511. 1941.

Common to locally abundant in seasonally humid/inundated savanna; palatable (3); flowering December (*January*) to February; $2n = 20$, meiosis normal; possibly the diploid progenitor of the apomictic species of sect. *Plicatula*. Distribution: Paraguay and Brazil. (698, 809, 816, 862, 863, 1622, 1669, 1812, 2003, **2276**, 2453)

P. macedoi Swallen, Phytologia 14(6): 377. 1967.

The type of the species has 3–4 racemes 12–16 cm long; material from Chiquitanía is similar in spikelet morphology, but inflorescences tend to be somewhat pyramidal (racemes 2–10 cm long). Occasional in *cerrado*, particularly on lateritic crests; flowering January (*February*) to March. Distribution: central Brazil. (617, 714, 1643, 1781, 1796, 1797, 1827, 2323)

P. plicatulum Michx., Fl. Bor. Amer. 1: 45. 1803. *P. multiflorum* Desv., Opusc. Sci. Phys. Nat. 58. 1831. *P. montevidense* Sprengel, Syst. Veg. 1: 246. 1825. *P. saxatile* Salzm. ex Doell in Mart., Fl. Bras. 2(2): 76. 1877, nomen nudum. *P. plicatulum* var. *longipilum* Hack., Feddes Repert. Spec. Nov. Regni Veg. 6: 342. 1909.

This variant most closely resembles the type fragment of the species (sensu lato), as well as more recent collections from the southern United States where the type collection was made. Different populations (genotypes) possibly originated separately via polyploidization and apomixis from diploid genotype(s) or from existing but distinct apomictic populations. Although it is common in most *cerrado* localities, it is locally abundant in ungrazed savannas. The more pubescent genotypes provide the best forage of any native grass in *cerrado* communities; palatable (3–4). Populations flower from January to (*March, April*) May. Local names: *gamalote, camalote, gramalote*. Distribution: southern United States to Argentina. (769, 867B, 1657, 1840, 1854, 1865, 1876, 1878, 1917, 1993, 2390, 2444, 2455)

Pennisetum Rich.

Brunken, J. 1977. A systematic study of *Pennisetum* sect. *Pennisetum* (Gramineae). Amer. J. Bot. 64: 161–176. Parodi, L. R. 1925. Las Gramineae del género *Pennisetum*. Anales Mus. Nac. Hist. Nat. Buenos Aires 32: 501–526.

KEY TO SPECIES

1a. Inner whorl of bristles ciliate; culms herbaceous, 2–5 mm in diameter.
  2a. Inner whorl of bristles flattened; spikelets 2–3 per involucre; panicles yellow or green ..... *P. ciliare*
  2b. Inner whorl of bristles terete; spikelets 1 per involucre; panicles purple ..... *P. setosum*
1b. Inner whorl of bristles not ciliate; culms stout, semiwoody, 5–10 mm in diameter.
  3a. Spikelet stipitate within the involucre; one bristle distinctly longer than the rest; panicles purple ..... *P. purpureum*
  3b. Spikelet sessile; bristles of various lengths but one not distinctly longer than the rest; panicles yellow ..... *P. nervosum*

P. ciliare (L.) Link., Hort. Berol. 1: 213. 1827. *Cenchrus ciliaris* L., Mant. 302. 1771; see DeLisle (1963) for extensive synonymy.

Cultivated forage grass adapted to the sandy soils of the Gran Chaco; flowering in October; local names: *bufel, bufelo*. (1258)

P. nervosum (Nees) Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 3: 177. 1835. *Gymnotrix nervosa* Nees, Agrost. Bras. 277. 1829. *Cenchrus nervosus* (Nees) Kuntze, Rev. Gen. Pl. 3(3): 347. 1898.

Rare, roadside embankment; flowering in January. Distribution: Ecuador, Argentina, and Brazil. (1690)

P. purpureum Schum., Beskr. Guin. Pl. 44. 1827.

Cultivated forage grass of African origin; due to its robust stature and stout woody culms, the forage must be harvested by hand and fed to cattle; utilized to a limited extent on almost all estancias; local names: mercurón, elefante. (979)

P. setosum (Sw.) L. Rich. in Pers., Syn. Pl. 1: 72. 1805. *Cenchrus setosus* Sw., Prodr. 26. 1788. *Panicum cenchroides* L. Rich., Actes Soc. Hist. Nat. Paris 1: 106. 1792, non Lam., 1798 nec Elliott, 1816. *Pennisetum pallidum* Nees, Agrost. Bras. 285. 1829.

Similar to *P. polystachyon* (L.) Sw., an Old World annual species; however, material from Chiquitanía is clearly perennial with short, stout rhizomes. Occasional in scrub on margins of granitic outcrops, rarely in *cerrado*; flowering December to July. Distribution: Mexico and the West Indies to Brazil; Bolivia: the Yungas. (635, 839, 1821, 2007)

Pharus R. Browne

Judziewicz, E. J. 1987. Taxonomy and morphology of the tribe Phareae. Ph.D. Dissertation. Univ. of Wisconsin, Madison, Wisconsin.

P. lappulaceus Aubl., Hist. Pl. Guiane 2: 859. 1775. *P. glaber* H.B.K., Nov. Gen. Sp. 1: 196. 1816. *P. pubescens* Sprengel, Neue Entdeck. Pflanzenk. 1: 241, p. 1, f. 1–4. 1820. *P. brasiliensis* Raddi, Agrost. Bras. 21. 1823. *P. micranthus* Schrader ex Nees, Agrost. Bras. 302. 1829. *P. angustifolius* Doell in Mart., Fl. Bras. 2(2): 23. 1871. *P. latifolius* L. var. *parviflorus* (Doell) Prodoehl, Bot. Arch. 1: 250. 1922.

Occasional, in deep shade of seasonal forest. Distribution: Mexico and the West Indies to Argentina; Bolivia: the Yungas. (547, 676, 832, 1773, 1890, 1965)

Rhipidocladum McClure

R. racemiflorum (Steudel) McClure, Smithson. Contr. Bot. 9: 106. 1973. *Arthrostylidium racemiflorum* Steudel, Syn. Pl. Glumac. I: 336. 1854.

Occasional, a liana in seasonal forest; palatable (3); local name: *taquara*. Distribution: Central America to Peru; Bolivia: the Yungas. (729, 751, 2447, 2734)

Rhynchelytrum Nees

R. repens (Willd.) C. E. Hubb., Bull. Misc. Inform. (1934): 110. 1934. *Saccharum repens* Willd., Sp. Pl. 1: 322. 1791. *Tricholaena rosea* Nees, Linnaea 11: 129. 1837. *R. roseum* (Nees) Stapf & C. E. Hubb. 9(5): 880. 1930.

Rare, roadside weed; flowering in October. Distribution: throughout the tropics. (2827)

Rhytachne Desv.

R. subgibbosa (Winkl. ex Hack.) W. D. Clayton, Kew Bull. 20: 261. 1966. *Rottboellia loricata* Trin. subsp. *subgibbosa* Winkl. ex Hack. in Mart., Fl. Bras. 2(3): 311. 1883. *Rottboellia loricata* Trin. subsp. *glaberrima* Hack. in Mart., Fl. Bras. 2(3): 311. 1883.

Rare, San Ignacio de Velasco. Distribution: Brazil, Paraguay, and Argentina. (*Bruderreck 149* ISC, LPB)

Saccharum L.

Molina, A. M. 1981. El genero *Erianthus* (Gramineae) en la Argentina y paises limítrofes. Darwiniana 23: 559–585. Swallen, J. 1966. Notes on grasses. Phytologia 14(2): 91–95.

KEY TO SPECIES

1a. Spikelets awned, 6–8 mm long; rachis internodes ½–⅔ the length of the spikelet; foliage basal, the sheaths strictly equitant and covered with a thick, chalky wax ..... *S. trinii*

1b. Spikelets awnless, 3.5–4.5 mm long; rachis internode as long as or twice the length of the spikelet; foliage cauline, the sheaths rounded on the back, not covered with chalky wax ..... *S. officinarum*

S. officinarum L., Sp. Pl. 54. 1753.

Sugar cane, cultivated on a small scale in Chiquitanía for sugar production and fodder for livestock, particularly pigs; cultivated commercially on the alluvial plains near Santa Cruz de la Sierra; flowering April to July. (2120, 2445)

S. trinii (Hack.) Renv., Kew Bull. 39: 184. 1984. *S. saccharoides* var. *trinii* Hack. in Mart., Fl. Bras. 2(3): 258. 1883. *Erianthus trinii* (Hack.) Hack. in A. DC., Monogr. Phan. 6: 135. 1889. *E. balansae* Hack. in A. DC., Monogr. Phan. 6: 133. 1889. *E. purpureus* Swallen, Phytologia 14: 92. 1966. *E. gla-*

brinodis (Hack.) Swallen, Phytologia 14: 93. 1966.

Individuals are variable within and between populations in their foliage vestiture (velutinous to scabrous) and spikelet pubescence (glumes villous, ciliate, or glabrous; callus hairs less than or surpassing the glumes). When burned, populations flower en masse within four weeks producing purple, chasmogamous spikelets on racemose, exserted panicles. Unburned populations bloom irregularly from December to May, producing pale tan, cleistogamous spikelets in globose panicles, which are included or only slightly exserted from the sheaths. These variants intergrade, and intermediate individuals have been observed in wet savannas which were only superficially burned and along the interface of burned and unburned savanna patches. Zonally abundant on valley-side *campos* (downslope) and in savanna marsh (providing more than 25% of the herbaceous cover), occasional in seasonally inundated savanna, seasonal ponds, and laguna margins; unpalatable (0). Distribution: Mexico to Argentina; Bolivia: the Beni and the Yungas. (cleistogamous phenotypes: 646, 767, 1787, 1806, 2281, 2589; chasmogamous phenotypes: 590, 1340, 2219; intermediate phenotypes: 1135, 1460, 2776)

Sacciolepis Nash

KEY TO SPECIES

1a. Foliage succulent, reddish, the blades flat; panicles 10–30 cm long; spikelets glabrous, nerves of glumes and lower lemma indurate ..... *S. myuros*
1b. Foliage not succulent, green, the blades involute; panicles 6–8 cm long; spikelets glabrous or hirsute, nerves of glumes and lower lemma not indurate ..... *S. angustissima*

S. angustissima (Hochst.) Kuhlm., Comiss. Linhas Telegr. Estratég. Mato Grosso Amazonas 67, Annexo 5, Bot. 11: 92. 1922. *Panicum angustissimum* Hochst. ex Steudel, Syn. Pl. Glumac. 1: 66. 1854. *S. karsteniana* Mez, Feddes Repert. Spec. Nov. Regni Veg. 15: 123. 1918.

Common to locally abundant, valley-side *campos* (midslope), seasonally inundated savannas, savanna marshes and seasonal ponds; flowering March to (*May*) June, and irregularly throughout the year; $2n = 36$. Distribution: Venezuela and the Guianas to central Brazil. (593, 688, 902, 1136, 1198, 1325, 1429, 1641, **1871,** 1946, 2027, 2452)

S. myuros (Lam.) Chase, Proc. Biol. Soc. Wash. 21: 7. 1908. *Panicum myuros* Lam., Tabl. Encycl. 1: 172. 1791.

Common, seasonally inundated or humid savannas, valley-side *campos*, and seasonal ponds; usually along cow paths; flowering November to (*May*) July. Distribution: Mexico to Brazil and Paraguay; Bolivia: Andean Piedmont of Santa Cruz, Chapare, Beni, and the Yungas. (889, 1117, 1253, 2022, 2119, 2603)

Schizachyrium Nees

Türpe, A. M. 1983. Revision of the South American species of *Schizachyrium* (Gramineae). Kew Bull. 39: 169–178.

KEY TO SPECIES

1a. Racemes flexuous, the rachis internodes and pedicels recurved ..... *S. microstachyum*
1b. Racemes straight, the rachis internodes and pedicels not recurved, erect and appressed to the spikelet.
  2a. Blades 2–7 cm long; rachis internodes delicate, 0.2–0.6 mm wide at apex; annuals or of indefinite duration, decumbent or scandent; foliage strictly cauline.
    3a. Culms profusely branched above to form a compound panicle of numerous exserted racemes; rachis internodes about 0.2 mm wide at apex; sessile spikelet 3 mm long, the lower glume with a medial groove or dark line ..... *S. sulcatum*
    3b. Culms sparsely branched; racemes few to several, not exserted and borne singly at the nodes of the culm; rachis internodes 0.4–0.6 mm wide at apex; sessile spikelet 4 mm long, the lower glume rounded on the back ..... *S. maclaudii*
  2b. Blades 10–70 cm long; rachis internodes 0.8–1.0 mm wide at apex; caespitose perennials; foliage basal and cauline.
    4a. Racemes solitary (rarely 2), terminal, exserted; pedicellate spikelet 3–6 mm long, awnless, strongly nerved; foliage strictly basal ..... *S. tenerum*
    4b. Racemes 4–50 borne at the upper nodes, the base usually included in the sheath; pedicellate spikelets 0.5–2.5 mm long, subaristate, not strongly nerved; foliage basal and cauline.
      5a. Lower glume of sessile spikelet strongly concave, coriaceous ..... *S. sanguineum*
      5b. Lower glume of sessile spikelet flat or weakly concave, cartilaginous or chartaceous.
        6a. Lower glume of sessile spikelet scabrous, cartilaginous; pedicellate spikelet up to 1 mm long ..... *S. scabriflorum*
        6b. Lower glume of sessile spikelet smooth, chartaceous; pedicellate spikelet 2–2.5 mm long ..... *S. beckii*

FIGURE 6. *Schizachyrium beckii* (*Killeen 1987*).—A. Habit and compound inflorescence (bar = 5 cm).—B. Spikelet pair (bar = 1.5 mm).—C. Lower glume of the sessile spikelet (bar = 1 mm).

S. beckii Killeen, sp. nov. TYPE: Bolivia. Santa Cruz: Serranía de San Lorenzo 10 km W of San Javier, Prva. Ñuflo de Chavez, 16°15′S, 62°40′W, 900 m, 17 Apr. 1986, *Killeen 1987* (holotype, ISC; isotypes, LPB, F, MO, US, ISC). Figure 6.

S. sanguineum (Retz.) Alston affinis sed culmis ramificantibus copiose ad nodos superos formantibus paniculas compositas elongatas, 40–60 racemis spathiformibus; spathis 1.5–2.0 cm longis; racemis 1 3 cm longis, spiculis 4–6 binatim; internodiis rachidium 3.0–3.5 mm longis, callis minutis 0.3 mm longis, non induratis valde; glumis infernis lanceolatis, planis, chartaceis, nec convexis nec coriaceis, 0.7 mm latis notabilis.

Caespitose perennial bunch grass; innovations intravaginal; culms solid, 4.5 mm wide, compressed, glabrous, smooth, branched at the upper nodes. Foliage basal and cauline; sheaths glabrous, keeled, strongly equitant, longer than the internodes; ligule membranous, 2 mm long; blades flat

TABLE 5. Morphological variation for selected characters in the *Schizachyrium microstachyum* complex.

Specimen[1]	Panicle	Rachis internodes	Spikelet size (mm)	Habitat preference	Flowering phenology	Latitude	Region
2594	elongate	strongly recurved	4	seasonally humid	July	14°35′S	Beni
1572	elongate	weakly recurved	5–6	well drained	January	17°40′S	Andean Piedmont of Santa Cruz
1566	corymbose	strongly recurved	4	seasonally humid	January	17°40′S	Andean Piedmont of Santa Cruz
724	corymbose	strongly recurved	4	seasonally humid	January	16°05′S	Chiquitanía
2475	elongate	weakly recurved	4–5	well drained	May	16°05′S	Chiquitanía

[1] All specimens those of the author.

or folded, glaucous, up to 23 cm long, reduced at the upper nodes, abruptly narrowed at the base, the junction between the blade and the sheath indistinct, the apex carinate. Inflorescence an elongate, compound panicle of spatheate racemes; spathes 1.5–2 cm long; racemes of 4–6 pairs of spikelets, 1–3 cm long, not exserted; rachis internodes ciliate, 3–3.5 mm long, broadest at the apex, narrowed at the base, coriaceous, not inflated; pedicels slender, flattened, 2.5–3 mm long, 1 mm wide; the rachis internode and pedicel united at base to form a short callus 0.3 mm long, the callus hairs 1 mm long. Sessile spikelet 5 mm long, inclusive of the callus; lower glume as long as the spikelet, lanceolate, chartaceous, dorsally compressed, flat, 0.7 mm wide, with 2 submarginal, minutely scabrous keels, the apex minutely bidentate, the midnerve suppressed; upper glume laterally compressed, keeled, 4.5 mm long, 0.5 mm wide when folded; lower lemma hyaline, similar to the lower glume, the palea lacking; upper lemma hyaline, 3.5 mm long, awned from between two lobes 2.5 mm long, the awn 17 mm long, 1-geniculate, the palea vestigial, 0.2 mm long; lodicules 2, truncate, evidently nerved; stamens 3, the anthers 2 mm long, reddish; style branches 2, naked at base, the stigmas plumose, 1.5 mm long. Pedicellate spikelet vestigial, 2–2.5 mm long, 0.2 mm wide, a single awned bract, the awn 2.5 mm long, inserted between 2 minute teeth.

This species is allied to the *S. sanguineum* complex but has smaller spikelets 5 mm (vs. 6.5–8 mm) long, the flat, chartaceous lower glume of the sessile spikelet (vs. strongly convex and coriaceous), a callus 0.3 (vs. 0.5–1) mm long, and the highly branched compound panicle with 40–60 (vs. 5–25) racemes. Similar in some respects to *S. riedelii* var. *multirameus* Hack., with which it shares the large compound panicle; however, the latter species has the strongly convex, coriaceous lower glume typical of *S. sanguineum* s.l. Locally abundant in *campo rupestre* and occurring with typical variants of *S. sanguineum* (i.e., *Killeen 1985*).

S. maclaudii (Jacques-Félix) S. T. Blake, Proc. Roy. Soc. Queensland 80(6): 78. 1969. *S. brevifolium* var. *maclaudii* Jacques-Félix, Rev. Inst. Bot. Appl. Agric. Trop. 32: 432, f. 5b. 1953.

Similar to *S. brevifolium* (Sw.) Nees, which has smaller spikelets (3 vs. 4 mm), slender rachis internodes (0.2 vs. 0.6 mm wide at apex), and shorter (2–4 cm vs. 3–8 cm), more blunt leaf blades; in addition, some specimens from Chiquitanía have a glabrous callus similar to local forms of *S. sulcatum*. Inconspicuous, in rank vegetation of seasonally inundated savanna or shallowly rooted in superficial soils of granitic outcrops (plants then caespitose and annual); flowering *May* to July. Distribution: northern South America and Brazil. (915, 2084, 2606)

S. microstachyum (Desv. ex Ham.) Roseng., Arrill. & Izag., Bol. Fac. Agron. Montevideo. 103: 35. 1968. *Andropogon microstachyus* Desv. ex Ham., Prodr. Pl. Ind. Occid. 8. 1825. *A. scoparius* C. Presl, Rel. Haenk. 1: 338. 1830, non Michx., 1803. *A. paniculatus* Kunth, Enum. Pl. 1: 494. 1833, non Lam., 1778. *A. lhotzkyi* Steudel, Syn. Pl. Glumac. 384. 1855. *Andropogon condensatus* subsp. *elongatus* Hack. in Mart., Fl. Bras. 2(3): 297. 1883. *S. paniculatum* (Kunth) Herter, Revista Sudamer. Bot. VI (5–6): 135. 1940. *S. neoscoparium* Herter, Revista Sudamer. Bot. VI (6–8): 193. 1943. *S. microstachyum* subsp. *elongatum* (Hack.) Roseng., Arrill. & Izag., Bol. Fac. Agron. Montevideo 103: 37. 1968.

A polymorphic species complex with numerous intergrading geographic races and ecotypes. In eastern Bolivia four phenotypes with distinct morphology, phenology, and habitat distribution have been documented (Table 5). Common in *cerrado* throughout Chiquitanía, as well as in well-drained and seasonally humid savannas with sandy soils of the Andean Piedmont and the seasonally humid savannas with heavy clay soils in the Beni; palatable (4); flowering April to (*May*) July in Chiquitanía; $2n = 20$. Distribution: Central America to Argentina and Uruguay. (Chiquitanía: 724, 859, 875, 896, 990, 1093, 1121, 1273, 1509, 1552, 1572, 1816, 1842, 2012, 2058, 2289, 2475, **2483**; Beni: 2594; Andean Piedmont of Santa Cruz: 1566, 1572, 2289, 2296; Steinbach 6809, 6950, 6951, 6952, 6953 US)

S. sanguineum (Retz.) Alston, Suppl. Fl. Ceylon 334. 1931. *Rottboellia sanguinea* Retz., Observ. Bot. 3: 25. 1783. *S. hirtiflorum* Nees, Agrost. Bras. 334. 1829. *S. semiberbe* Nees, Agrost. Bras. 336. 1829. *Andropogon hirtiflorus* (Nees) Kunth, Révis. Gramin. 2(39). 1832. *A. semiberbis* (Nees) Kunth, Révis. Gramin. 2(39). 1832. *A. riedelii* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 2: 263. 1832. *S. riedelii* (Trin.) A. Camus, Ann. Soc. Linn. Lyon 70: 88. 1923. *S. weberbaueri* Pilger, Notizbl. Bot. Gart. Berlin-Dahlem 8: 452. 1923.

Plants vary in foliage vestiture, the length/width ratio of leaf blades, pubescence of racemes, and the form of the lower glume of the sessile spikelet. Monomorphic populations with glabrous racemes are zonally abundant upslope in valley-side *campos* (*S. semiberbe* sens. str.), while *cerrado* populations are polymorphic and are composed of a mixture of intergrading genotypes each with a unique phenology. Typically, a colony with some distinctive trait (such as glaucous foliage or densely pubescent racemes) is associated with a restricted area of gravel soils developed over a laterite crest, while another genotype is randomly distributed in the well-drained, red clay soils common to *cerrado* communities; palatability between genotypes is variable (3–4); flowering January (*February to May*) to July; $2n = 50–60$, an abnormal meiosis indicates that the species is apomictic. Distribution: throughout the tropics but the greatest morphological diversity is found in the New World; Bolivia: Beni and the Yungas, absent from the savannas of the Andean Piedmont of Santa Cruz. (Pubescent variants: *S. hirtiflorum* (sens. str.): 1010, 1551, 2010, 2093, 2476, 2479, **2486,** 2629; glabrous variants: *S. semiberbe* (sens. str.): 732, 855, 1636, 1783, 1835, **1851,** 2018, 2026, 2095, **2421, 2442**; intermediate variants: 909, 1390, 1960, 1985, 1997, 2094, 2485, 2629)

S. scabriflorum (Rupr. ex Hack.) A. Camus, Ann. Soc. Linn. Lyon 70: 89. 1923. *Andropogon scabriflorus* Rupr. ex Hack. in Martius, Fl. Bras. 2(3): 299. 1883.

Occasional in *cerrado*; palatable (4); flowering January to (*February*) May; $2n = 40$. Distribution: central Brazil. (857, 879, 1619, 1772, 1829, 1852, 1996, **2328**)

S. sulcatum (Ekman) S. T. Blake, Proc. Roy. Soc. Queensland 80(6): 78. 1969. *Andropogon sulcatus* Ekman, Ark. Bot. 10(7): 4, p. 1, f. 3 & p. 6, f. 3. 1911. *A. brevifolius* var. *leptanthus* Hack. in A. DC., Monogr. Phan. 6: 364. 1889.

Rare, seasonally humid savanna near San Ignacio de Velasco; flowering in February. Distribution: Colombia and Brazil; Bolivia: the Beni. (*Bruderreck 195* ISC, LPB)

S. tenerum Nees, Agrost. Bras. 336. 1829. *S. filiforme* Nees, Agrost. Bras. 338. 1829. *Andropogon gracilis* C. Presl, Rel. Haenk. 1(4/5): 336. 1830, non Sprengel, 1825. *A. preslii* Kunth, Révis. Gramin. 2(32): 489. 1831. *A. tener* (Nees) Kunth., Révis. Gramin. 2(39): 565. 1832. *A. neesii* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 2: 264. 1832, non Kunth, 1832. *A. campestris* Kunth, Révis. Gramin. 3(41–44): 617. 1833.

Rare, seasonally humid savanna and valley-side *campo*; flowering February to March. Distribution: Central America to Argentina; Bolivia: Andean Piedmont of Santa Cruz and the Yungas. (1775, 1802, 1831)

Setaria P. Beauv.

KEY TO SPECIES

1a. Leaf blades pleated, palmlike, 4–15 cm wide; spikelets about 3 mm long ..... *S. poiretiana*
1b. Leaf blades not pleated, 0.3–3 cm wide; spikelets 1.5–2.5 mm long.
  2a. Bristles with retrorse scabrosities at tips, as well as antrorse scabrosities below, the panicles adhering to clothing ..... *S. scandens*

2b. Bristles antrorsely scabrose only, the panicles not adhering to clothing.
3a. Pedicels adnate to 5 or more bristles ..... *S. parviflora*
3b. Pedicels adnate to a single bristle.
4a. Leaves with an external ligule or ridge of thickened tissue on the abaxial surface at the junction of the blade and sheath, the blades 1–3 cm wide ..... *S. vulpiseta*
4b. Leaves lacking an external ligule, the blades 0.5–1.5 cm wide.
5a. Upper floret strongly rugose, broadly ovate; annuals ..... *S. fiebrigii*
5b. Upper floret smooth or weakly rugose, elliptic; perennials ..... *S. leiantha*

S. fiebrigii R. Herrm., Beitr. Biol. Pflanzen 10: 30. 56. 1910.

Occasional weed in sandy soils near San José de Chiquitos; flowering January to February? Distribution: Brazil, Paraguay, and Argentina; Bolivia: the Gran Chaco. (1286, 1697, 1698, 1703)

S. leiantha Hack., Anales Mus. Nac. Hist. Nat. Buenos Aires 4: 78. 1904. *S. argentina* R. Herrm., Beitr. Biol. Pflanzen 10: 30, 56. 1910. *Chaetochloa argentina* (Herrm.) Hitchc., Contr. U.S. Natl. Herb. 24(8): 480. 1927.

Occasional, as a weed in San José de Chiquitos. Distribution: Paraguay, Argentina, and Uruguay; Bolivia: Cochabamba and the Gran Chaco. (1260, 1706)

S. parviflora (Poir.) Kerguélen, Lejeunia 120: 161. 1987. *Cenchrus parviflorus* Poir. in Lam., Tabl. Encycl. 6: 52. 1804. *S. geniculata* (Lam.) P. Beauv., Ess. Agrostogr. 51, 178. 1812. *S. gracilis* H.B.K., Nov. Gen. Sp. 1: 109–110. 1816. *S. purpurascens* H.B.K., Nov. Gen. Sp. 110. 1816. *P. imberbis* Poir. in Lam., Encycl. Suppl. 4: 272. 1816. *S. imberbis* (Poir.) Roemer & Schultes, Syst. Veg. 2: 891. 1817. *P. flavum* Nees, Agrost. Bras. 238. 1829. *P. dasyurum* Nees, Agrost. Bras. 238. 1829. *P. penicillatum* Willd. ex Nees, Agrost. Bras. 238. 1829. *Chaetochloa geniculata* (Lam.) Millsp. & Chase, Field. Mus. Nat. Hist., Bot. Ser. 3: 37. 1903.

A pantropical species which varies in a number of characters when studied over its entire geographic range. In eastern Bolivia, the typical (more variable) variant occurs in well-drained habitats as a common weed. However, a well-defined genotype characterized by elongate internodes, glaucous foliage, and reduced bristles is restricted to seasonally inundated savannas. The short-bristled variant has a chromosome number of $2n = 72$; previous reports for the species are $2n = 18$ and 36 (Gould, 1960). Distribution: throughout the tropics. (common variant: 525, 588, 679, 711, 1507, 1710, 1766, 1814, 1627, 2227, 2273, 2389; short-bristled variant: 645, 1245, 1499, 1628, 2116, 2259, **2274**, 2327)

S. poiretiana (Schrader) Kunth, Révis. Gramin. 1: 47. 1829. *Panicum elongatum* Poir. in Lam., Encycl. Suppl. 4: 278. 1816, non Salisb., 1824 nec Pursh, 1814. *P. poiretianum* Schultes, Mant. 2: 229. 1824. *P. flabellatum* Steudel, Syn. Pl. Gram. 53. 1854. *Chaetochloa poiretiana* (Schultes) Hitchc., Contr. U.S. Natl. Herb. 22: 159. 1920.

Rare, logging roads in seasonal forests; flowering December to March. Distribution: Central America to Brazil; Bolivia: the Yungas, Chapare, and Cerro Amboró in western Santa Cruz. (680, 1856)

S. scandens Schultes, Mant. 2: 279. 1824. *S. trinii* Kunth, Enum. Pl. 1: 151. 1833. *Panicum scandens* var. *vulgare* Doell in Mart., Fl. Bras. 2(2): 171. 1877. *Chaetochloa scandens* (Schultes) Scribn. in J. D. Smith, Pl. Guatem. 5: 91. 1899.

Occasional, as a weed in savanna and forest soils. Distribution: Mexico to Paraguay; Bolivia: the Yungas. (804, 807, 838, 866)

S. vulpiseta (Lam.) Roemer & Schultes, Syst. Veg. 2: 495. 1817. *Panicum vulpisetum* Lam., Encycl. 4: 735. 1798. *S. composita* H.B.K., Nov. Gen. Sp. 1: 111. 1816. *Chaetochloa vulpiseta* (Lam.) Hitchc. & Chase, Contr. U.S. Natl. Herb. 18: 350. 1917.

Individuals of this species vary in stature, the length/width ratio of leaf blades, and size of inflorescence; however, the external ligule is characteristic. Common, in forest scrub, on forest/savanna margins, and as a weed along roads in forest soils; rarely occurring in the deep shade of seasonal forest; flowering January to (*March*) July. Distribution: Mexico to Paraguay; Bolivia: Andean Piedmont of Santa Cruz and the Beni. (829, 834, 847, 999, 1079, 1674, 1744, 1884, 2106, 2318)

Sorghastrum Nash

Dávila, P. A. 1988. Systematic revision of the genus *Sorghastrum* (Poaceae, Andropogo-

neae). Ph.D. Dissertation. Iowa State Univ., Ames, Iowa.

KEY TO SPECIES

1a. Awns stout, 5–10 cm long, pubescent, 2-geniculate; spikelets 7–9 mm long, the callus pungent ..... *S. minarum*
1b. Awns delicate, 1–8 mm long, glabrous, twisted or 1-geniculate; spikelets 3.5–4.5 mm long, the callus blunt ..... *S. setosum*

S. minarum (Nees) Hitchc., Contr. U.S. Natl. Herb. 24: 501. 1927. *Trachypogon minarum* Nees, Agrost. Bras. 349. 1829. *Andropogon minarum* (Nees) Kunth, Révis. Gramin. 2(33): 507. 1831. *Stipa penniglumis* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 1: 77. 1831. *Sorghum minarum* (Nees) Hack. in Mart., Fl. Bras. 2: 276. 1883. *Chrysopogon minarum* (Nees) Benth., J. Linn. Soc., Bot. 9: 73. 1881.

Similar to *S. balansae* Hack., which has an open panicle, a smaller callus (1 mm vs. 2.5 mm) and shorter awn (1.5–2.5 mm vs. 6–8.5 cm). Uncommon, *cerrado* and along *cerrado*/forest margins; flowering February to (*April*) May; $2n = 20$. Distribution: Brazil, Paraguay, and Argentina; Bolivia: Andean Piedmont of Santa Cruz. (1768, 1843, 1994, **2387**)

S. setosum (Griseb.) Hitchc., Contr. U.S. Natl. Herb. 12(6): 195. 1909. *Sorghum parviflorum* Desv. ex Ham., Prodr. Pl. Ind. Occid. 12. 1825, non P. Beauv., 1812. *Trachypogon stipoides* (H.B.K.) Nees var. *beta* Nees, Agrost. Bras. 351. 1829. *Andropogon setosus* Griseb., Cat. Pl. Cub. 235. 1866. *A. francavillanus* Fournier, Mex. Pl. 2: 56. 1881. *A. agrostoides* Speg., Anales Soc. Ci. Argent. 16: 136. 1883. *S. nutans* subsp. *micranthum* var. *submuticus* (Hack.) Hack. in Mart., Fl. Bras. 2(3): 275. 1883. *Sorghastrum parviflorum* (Desv.) Hitchc. & Chase, Contr. U.S. Natl. Herb. 18: 287. 1917. *S. stipoides* (H.B.K.) Nash. subsp. *agrostoides* (Speg.) Roseng., Arrill. & Izag., Gram. Urug. 201. 1970.

Occasional, in valley-side *campo*, savanna marsh, and seasonally humid savanna but locally abundant in some seasonally inundated savannas; flowering January (*February*) to May; $2n = 20$. Distribution: Central America to Argentina; Bolivia: Andean Piedmont of Santa Cruz. (846, 861, 885, 1630, 1764, 1811, 1958, 1991, 2114, **2306**, 2382)

Sorghum Moench

KEY TO SPECIES

1a. Rhizomatous perennials; caryopsis concealed by the glumes ..... *S. halapense*
1b. Caespitose annuals; caryopsis usually bursting from the glumes ..... *S. bicolor*

S. bicolor (L.) Moench, Meth. Pl. 207. 1794. *Holcus bicolor* L. Mant. Pl. 2: 301. 1771.

Newly introduced forage sorghums are being used by large estancias for fattening cattle; local name: *sorgo, sorgo forrajero.* (2446)

S. halepense (L.) Pers., Syn. Pl. 1: 101. 1805. *Holcus halepensis* L., Sp. Pl. 1047. 1753.

Common, as a weed along roadsides, particularly in the fertile soils of the alluvial plains SW of the Brazilian Shield; an important source of forage on cattle drives, palatable (3); flowering October to January. Distribution: throughout the tropics. (692, 1314)

Sporobolus R. Br.

Clayton, W. D. 1965. The *Sporobolus indicus* complex. Kew Bull. 19: 287–295.

KEY TO SPECIES

1a. Inflorescence a pyramidal panicle, at least the lowermost branches verticillate.
  2a. Spikelets about 1.5 mm long; glumes and lemma white or translucent; caespitose annuals ..... *S. pyramidatus*
  2b. Spikelets 2.5–3.5 mm long; glumes and lemma golden-purple-colored; caespitose perennial bunch grasses.
    3a. Panicle branches reflexed or spreading at maturity; leaf blades involute, 1–3 mm wide ..... *S. cubensis*
    3b. Panicle branches ascending or flexuous; leaf blades flat or folded, 5–15 mm wide ..... *S. sprengelii*
1b. Inflorescence an open or contracted panicle; branches not verticillate, if several per node, then inserted on one side.
  4a. Spikelets 0.8–1 mm long; stamens 1; panicles open; delicate caespitose annuals ..... *S. monandrus*
  4b. Spikelets 1.5–2.5 mm long; stamens 3; panicles contracted or open; perennial bunch grasses.
    5a. Panicle branches strictly erect and appressed to axis ..... *S. indicus* var. *exilis*
    5b. Panicle branches ascending to spreading ..... *S. jacquemontii*

S. cubensis Hitchc., Contr. U.S. Natl. Herb. 12: 237. 1909.

Rare, sandy soils of transition zone between *cerrado* and valley-side *campo* (Santa Rosa de la Roca); flowering is dependent upon fire. Distribution: West Indies to Brazil. (2826)

S. indicus var. **exilis** (Trin.) Koyama, J. Jap. Bot. 37: 235. 1962. *Agrostis tenacissima* Jacq., Icon. Pl. Rar. 16. 1787, non L.f., 1781. *Vilfa tenacissima* sensu H.B.K., Nov. Gen. Sp. 1: 138. 1816. *Axonopus poiretii* Roemer & Schultes, Syst. Veg. 2: 318. 1817. *Vilfa exilis* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 6(1): 89. 1840. *Sporobolus berteroanus* (Trin.) Hitchc. & Chase, Contr. U.S. Natl. Herb. 18: 370. 1917. *S. poiretii* (Roemer & Schultes) Hitchc., Bartonia 14: 32. 1932.

Not yet collected in Chiquitanía but common as a pioneer species on the sand dunes of the Andean Piedmont; flowering throughout the year. Distribution: southern United States to Argentina; Bolivia: Andean Piedmont of Santa Cruz, Cochabamba, Beni, and the Yungas. (1116, 1582)

S. jacquemontii Kunth, Révis. Gramin. 2: 427, t. 127. 1831. *Vilfa jacquemontii* (Kunth) Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 6: 92. 1840. *S. indicus* sensu Hitchc., Contr. U.S. Natl. Herb. 24(8): 393. 1927.

Common, as a weed of roadsides and pastures, in forest or savanna soils; occasional, in well-drained or seasonally humid savannas; locally abundant in *cerrado* SW of San Javier; coarse but somewhat palatable (2); flowering October to (*November*) April. Distribution: United States to Argentina; Bolivia: Andean Piedmont of Santa Cruz, Cochabamba, Beni, and the Yungas. (596, 721, 746, 819, 1234, 1318, 1363, 1370, 1461, 1513, 2193, 2277)

S. monandrus Roseng., Arrill. & Izag., Bol. Fac. Agron. Univ. Montevideo 103: 12. 1968.

Common, rooted in superficial soils on granitic outcrops, occasionally in *cerrado* on lateritic crests; flowering September to May. Distribution: Brazil, Paraguay, Uruguay, and Argentina. (806, 914, 1230A, 1442, 1483, 1825)

S. pyramidatus (Lam.) Hitchc., U.S. Dept. Agr. Misc. Publ. 243: 84, f. 48. 1936. *Agrostis pyramidata* Lam., Tabl. Encycl. 1: 161. 1791. *Vilfa arguta* Nees, Agrost. Bras. 395. 1829. *Sporobolus argutus* (Nees) Kunth, Enum. Pl. 1: 215. 1833.

Rare, seasonal pond; flowering in February. Distribution: United States to Argentina; Bolivia: Cochabamba, Beni, and the Yungas. (1715)

S. sprengelii Kunth, Révis. Gramin. 1: 68. 1829. *Agrostis sporobolus* Sprengel, Nov. Prov. Hal. 46. 1819.

Part of an intergrading species complex that includes *S. cubensis* Hitchc., *S. adustus* (Trin.) Roseng., *S. aeneus* (Trin.) Kunth, *S. acuminatus* (Trin.) Hack., and *S. eximius* (Nees) Ekman. The only collection from Chiquitanía is intermediate to currently accepted concepts of *S. aeneus* and *S. sprengelii* and is provisionally placed in the latter. Locally abundant in sandy soils of *campo rupestre* (Serranía de Santiago); flowering is stimulated by (probably dependent upon) fire. Distribution: Brazil. (2791)

Streptochaeta Schrader ex Nees

Judziewicz, E. J. & T. R. Soderstrom. 1989. Morphological, anatomical, and taxonomic studies in *Anomochloa* and *Streptochaeta* (Poaceae: Bambusoideae). Smithson. Contr. Bot. 68: 1–52.

S. spicata Schrader ex Nees, Agrost. Bras. 537. 1829. *Lepideilema lancifolium* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 3: 172. 1840.

Rare, in deep shade of seasonal forest; flowering April and May. Distribution: Mexico to Argentina. (970, 1968)

Thrasya H.B.K.

KEY TO SPECIES

1a. Racemes 10–30 cm long; rachis 2–4 mm wide when folded, the margins glabrous; spikelets 5 mm long; upper floret concealed by the upper glume ..... *T. petrosa*

1b. Racemes 3–10 cm long; rachis 1–1.5 mm wide when folded, the margins ciliate or glabrous; spikelets about 3 mm long; upper floret not concealed by the upper glume.

2a. Rachis ciliate, the hairs stout, tuberculate-based, 1–1.5 mm long, turning yellow at maturity; bunch grass with intravaginal innovations; foliage basal ..... *T. thrasyoides*

2b. Rachis glabrous or ciliate, the hairs delicate, not tuberculate-based nor yellowing with age; caespitose with extravaginal innovations; foliage cauline ..... *T. crucensis*

FIGURE 7. *Thrasya crucensis* (*Killeen 2334*).—A. Base of plant.—B. Mid-portion of the culm.—C. Raceme (A, B, and C: bar = 5 cm).—D. Spikelet pairs and rachis.—E. Lower glume and lower lemma (D and E: bar = 1 mm).

T. crucensis Killeen, sp. nov. TYPE: Bolivia. Santa Cruz: granitic dome 1 km N of Rancho Puesto Nuevo, 35 km S of Concepción, Prva. Ñuflo de Chavez, 16°25′S, 62°00′W, 700 m, 26 Feb. 1987, *Killeen 2334* (holotype, ISC; isotypes, LPB, F, SP, MO, US, SI). Figure 7.

T. petrosa (Trin.) Chase, affinis sed innovationibus extravaginalibus, culmis ramificantibus copiose ad nodos medius faciens rami multi sterilis; foliis caulinis, ligulis 2–5 mm longis, laminis 2–4.5 mm latis; rachidibus racemorum 2.8 mm latis, marginalibus pilosis molliter, pilis 0.2–0.5 mm longis, spiculis 3.0 mm longis, lemmatibus inferior apex et basis pilosis glaber notabilis.

Caespitose perennial from extravaginal innovations, the rhizomes short. Culms terete, the internodes glabrous. Foliage cauline; sheaths longer than internodes, compressed, glabrous, auriculate;

auricles adnate to a membranous ligule 2–5 mm long; blades 4–25 cm long, 2–4 mm wide, linear, reduced at the upper nodes, revolute, glabrous. Inflorescence a single exserted raceme 5–15 cm long, the rachis foliaceous, 1.4 mm wide when folded, clasping the lower ⅓ of spikelets, the margins softly pilose with white hairs 0.2–0.5 mm long; spikelets 3 mm long, paired, unequally pedicellate, the pedicels adnate to the midrib, each pair oriented in a single row with the backs of the lower lemmas facing each other; disarticulation below the glumes. Lower glume narrowly triangular, 2 mm long, adnate to the first rachilla internode at the base, or reduced to a cupulate bead; upper glume narrowly lanceolate, acute, sparsely pubescent along the margins, equaling the upper floret but not covering the sides of the upper lemma; lower floret staminate, the lemma chartaceous, splitting lengthwise to the base along a medial groove, hispid apically on the two lateral keels, the palea equaling the lemma, glabrous, acuminate; upper floret 2.2 mm long, narrowly elliptic, the lemma indurate, stramineous, smooth, bearded at the apex, the margins inrolled, the palea similar in texture, free at apex.

The spikelet morphology of *T. crucensis* is similar to the widespread species *T. petrosa*; however, the plants of *S. crucensis* have branched culms with cauline foliage (vs. unbranched culms with basal foliage), racemes 5–9(12) cm long (vs. (10)15–30 cm long), rachis margins 1 mm wide (vs. 2–3 mm wide), and spikelets 3 mm long (vs. 4–5.5 mm long). Moreover, *T. crucensis* has a markedly different habitat preference and phenology. It is restricted to cracks and superficial soils on bald granitic domes (inselbergs), and flowers January to (*February*) March; $2n = 20$, the type population. (Paratypes: 808, 1819)

T. petrosa (Trin.) Chase, Proc. Biol. Soc. Wash. 24: 115. 1911. *Panicum petrosum* Trin., Sp. Gram. 3: 280. 1836. *Tylothrasya petrosa* (Trin.) Doell in Mart., Fl. Bras. 2(2): 296. 1877.

Individual plants differ in stature, foliage vestiture, length of racemes, width and color of rachis wings, and the presence or absence of cilia on rachis margins. Different variants occur in mixed populations; very palatable (4). Common, to locally abundant in ungrazed *cerrado*; flowering January to (*March*) June; abnormal meiosis indicates probable apomixis. Distribution: Central America to Paraguay; Bolivia: the Beni. (738, 871, 1736, 1784, 1850, 1953, 1988, 2391, 2393, 2418; *Cutler 7002* US)

T. thrasyoides (Trin.) Chase, Proc. Biol. Soc. Wash. 24: 114. 1911. *Panicum thrasyoides* Trin., Gram. Panic. 126. 1826. *T. hirsuta* Nees, Agrost. Bras. 94. 1829.

Locally abundant in *campo rupestre* (Serranía de San Lorenzo); flowering is dependent upon fire. Distribution: central Brazil. (2830)

Trachypogon Nees

T. plumosus (Humb. & Bonpl. ex Willd.) Nees, Agrost. Bras. 344. 1829. *Andropogon plumosus* Humb. & Bonpl. ex Willd., Sp. Pl. 918. 1806. *A. montufari* H.B.K., Nov. Gen. Sp. 1: 184. 1816. *T. montufari* (H.B.K.) Nees, Agrost. Bras. 342. 1829.

Locally abundant in Lomerio on rocky hillsides and ridgetops (*campo limpo*) and over lateritic crests; occasional in *campo cerrado* with deep red clay soils, in the sandy soils of seasonally humid savannas, and on valley-side *campos* (upslope); somewhat palatable (2); flowering inhibited by fire, November to (*January*) April; $2n = 20$. Distribution: Central America to Argentina; Bolivia: Tarija, Beni, Andean Piedmont of Santa Cruz, and the Yungas. (636, 637, 704, 777, 1448, 1617, 1651, 1758, 1776, 1817, **2310**)

Tripogon Roemer & Schultes

T. spicatus (Nees) Ekman, Ark. Bot. 11: 36. 1912. *Bromus spicatus* Nees, Agrost. Bras. 471. 1829. *Diplachne simplex* Doell in Mart., Fl. Bras. 2(3): 97. 1878. *D. spicata* (Nees) Doell in Mart., Fl. Bras. 2(3): 160. 1878. *Triplasis setacea* Griseb., Abh. Königl. Ges. Wiss. Gött. 24: 304. 1879. *Sieglingia spicata* (Nees) Kuntze ex Stuck., Anales Mus. Nac. Hist. Nat. Buenos Aires 11: 128. 1904. *Rabdochloa spicata* (Nees) Kuntze ex Stuck., Anales Mus. Nac. Hist. Nat. Buenos Aires 11: 121. 1904.

Common, superficial soils over granitic outcrops; flowering September to March. Distribution: United States to Argentina; Bolivia: Cochabamba. (812, 1224, 1463, 1543)

Tripsacum L.

de Wet, J. M. J., J. R. Harlan & D. E. Brink. 1982. Systematics of *Tripsacum dactyloides* (Gramineae). Amer. J. Bot. 69: 1251–1257.
de Wet, J. M. J., D. H. Timothy, K. W. Hilu & G. B. Fletcher. 1981. Systematics of South American *Tripsacum* (Gramineae). Amer. J.

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KEY TO SPECIES

1a. Culm internodes with lanulose tomentum; sheaths glabrous, pubescent or tomentose; staminate spikelets subsessile ..... *T. australe*

1b. Culm internodes and sheaths glabrous; staminate spikelets subsessile and pedicellate ..... *T. andersonii*

T. andersonii J. R. Gray, Phytologia 33: 204. 1976.

Introduced into the area in the 1970s as a forage grass by the Fundación Baviera-Boliviana but not widely adopted; a few *estancias* may still have remnant populations. Local name: *pasto guatemala*.

T. australe Cutler & E. S. Anderson, Ann. Missouri Bot. Gard. 28: 259. 1941.

Occasional, forest margins and scrub thickets around granitic outcrops; palatable (3); flowering December to (*February*) April; $2n = 36$. Distribution: Venezuela, Colombia, Brazil, and Paraguay; Bolivia: Beni and the Yungas. (793, **841,** 1815, 2004, **2326**; *Cutler 6007* US; *Cutler 6008* MO)

Zea L.

Z. mays L., Sp. Pl. 971. 1753.

The local cultivar 'Cubano Amarillo' is used as an animal feed and to make a sweet *chica*, which is a staple of the local diet.

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NOTES

A NEW SPECIES AND COMBINATION IN *THELYPTERIS* FOR GUYANA

Thelypteris (subg. *Goniopteris*) **schomburgkii** A. R. Smith, sp. nov. TYPE: Guyana: Essequibo, *Schomburgk 135* (holotype, K; isotype, K). Figure 1.

A *T. nephrodioides* (Klotzsch) Proctor pilis longioribus interdum acicularibus secus axes abaxialiter, indusio parvo inconspicuo, et venis late anastomosantibus infra sinum differt.

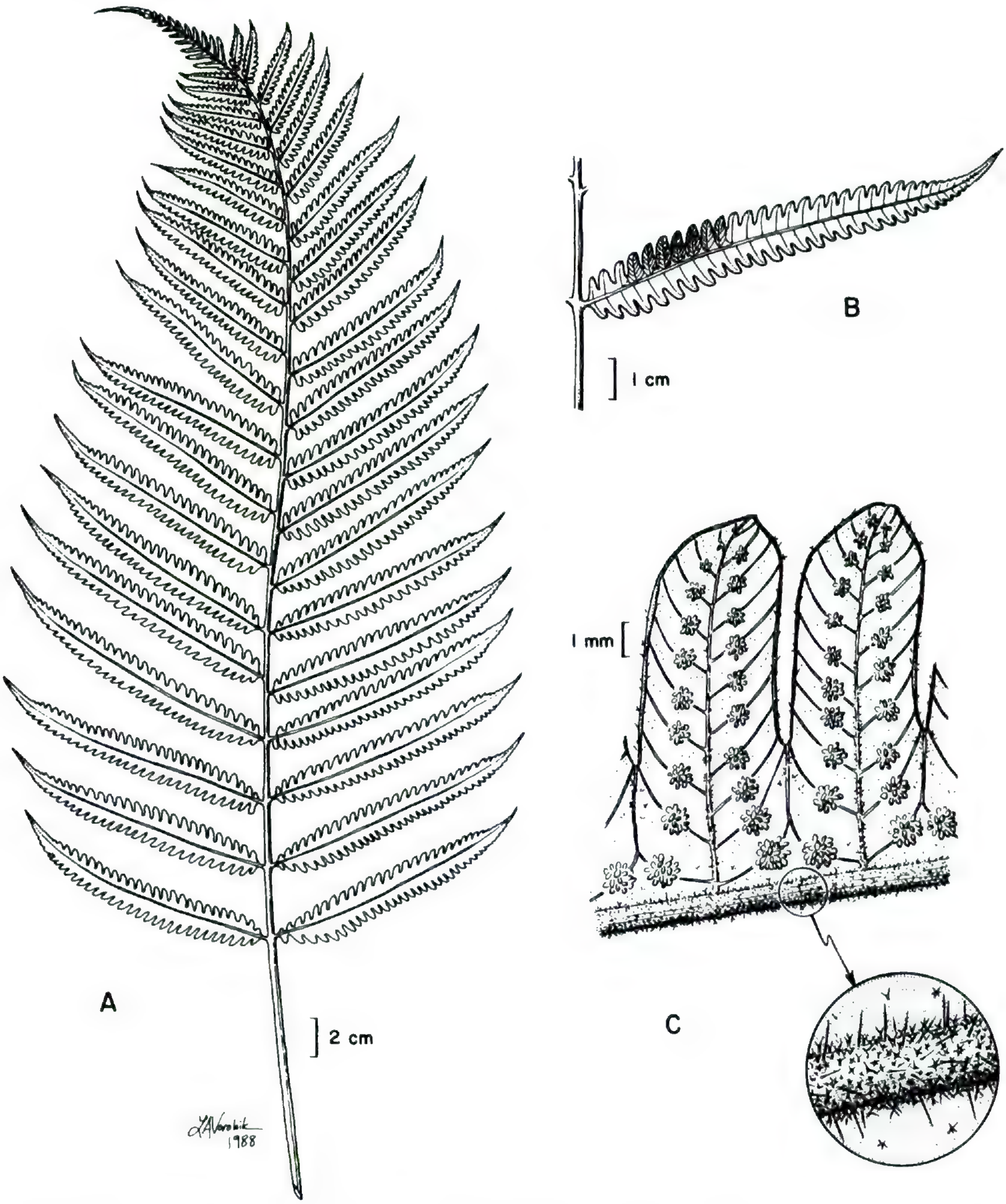

FIGURE 1. *Thelypteris schomburgkii*, based on the type and isotype.—A. Lamina and distal portion of stipe.—B. Pinna.—C. Segments, showing venation and indument, with detail of hairs.

Rhizome unknown. Fronds 60–70 cm long; lamina with a gradually reduced, confluent, pinnatifid apex, with 17–20 pairs of lateral pinnae, these to 15 × 2.2 cm, incised ca. ½–⅔ their width, truncate at base and with basal segments of larger pinnae reduced half or more; rachis buds lacking; segments rounded to truncate at the tip, with up to 14 pairs of veins, proximal pair of veins from adjacent segments uniting at an acute or obtuse angle with an excurrent vein to sinus; rachis, costae, and costules abaxially with dense, stellate, furcate, and acicular hairs intermixed, these 0.1–0.5 mm long, unbranched hairs the longest, branched hairs short-stalked; laminar tissue on both sides with sessile, appressed, stellate hairs, not verrucose. Sori inframedial, with a small, setose or furcate-hairy indusium.

Known only from the type collection, at low elevation.

This is probably most closely related to *T. nephrodioides* (Klotzsch) Proctor, but differs by having lighter green lamina, small inconspicuous indusium (large and persistent in *T. nephrodioides*), longer hairs along the axes abaxially (with many acicular unbranched hairs in addition to the stalked-stellate ones), and veins that are anastomosing at a broadly acute to obtuse angle below the sinus with an excurrent vein to the sinus. In this last character, *T. schomburgkii* comes closer to *T. biolleyi* (Christ) Proctor, which differs in having some long anchor-shaped hairs on the costae abaxially and in having obtusely united veins below the sinus.

Thelypteris (subg. *Goniopteris*) **gonophora** (Weath.) A. R. Smith, comb. nov. *Dryopteris gonophora* Weath. in A. C. Smith et al., Lloydia 2: 164, fig. 1(1–3). 1939. TYPE: Guyana: western extremity of Kanuku Mts. in drainage of Takutu River, *A. C. Smith 3283* (holotype, GH not seen, photo GH)

—Alan R. Smith, *University Herbarium, University of California, Berkeley, California 94720, U.S.A.*

STEYERMARKOCHLOA ANGUSTIFOLIA (SPRENGEL) JUDZIEWICZ, A NEW COMBINATION (POACEAE–ARUNDINOIDEAE–STEYERMARKOCHLOEAE)

The recent return to the U.S. National Herbarium of a loan of species of *Pariana* (Poaceae–Bambusoideae–Olyreae) included a fragment of the type of *Pariana angustifolia* Sprengel, which proved to be identical to the species described as *Steyermarkochloa unifolia* (Poaceae–Arundinoideae–Steyermarkochloeae) by Davidse & Ellis (Ann. Missouri Bot. Gard. 71: 994–1012. 1984). This was confirmed by examination of the IDC microfiche of B-WILLD sheet 18792. The following new combination is therefore required:

Steyermarkochloa angustifolia (Sprengel) Judziewicz, comb. nov. Based on *Pariana angustifolia* Sprengel, Syst. Veg. 2: 609. 1825. TYPE: Venezuela. Amazonas: Atabapo, *Humboldt s.n.* (holotype, B not seen; fragment US).

Steyermarkochloa unifolia Davidse & Ellis, Ann. Missouri Bot. Gard. 71: 995. 1984.

In addition to Venezuelan and Colombian populations cited by Davidse & Ellis (loc. cit.), the species is also known from nearby Amazonas, Brazil at São Felipe on the Rio Negro (*Fróes 28788*, US).

—Emmet J. Judziewicz, *Department of Botany, Smithsonian Institution, Washington, D.C. 20560, U.S.A.*

ANN. MISSOURI BOT. GARD. 77: 204. 1990.

CESTRUM NEBLINENSE (SOLANACEAE), A NEW SPECIES FROM VENEZUELA

During preparation of the family treatment of the Solanaceae for the upcoming *Flora of the Guayana Highlands* (Steyermark et al., in prep.), material of a distinctive and undescribed species of *Cestrum* was encountered.

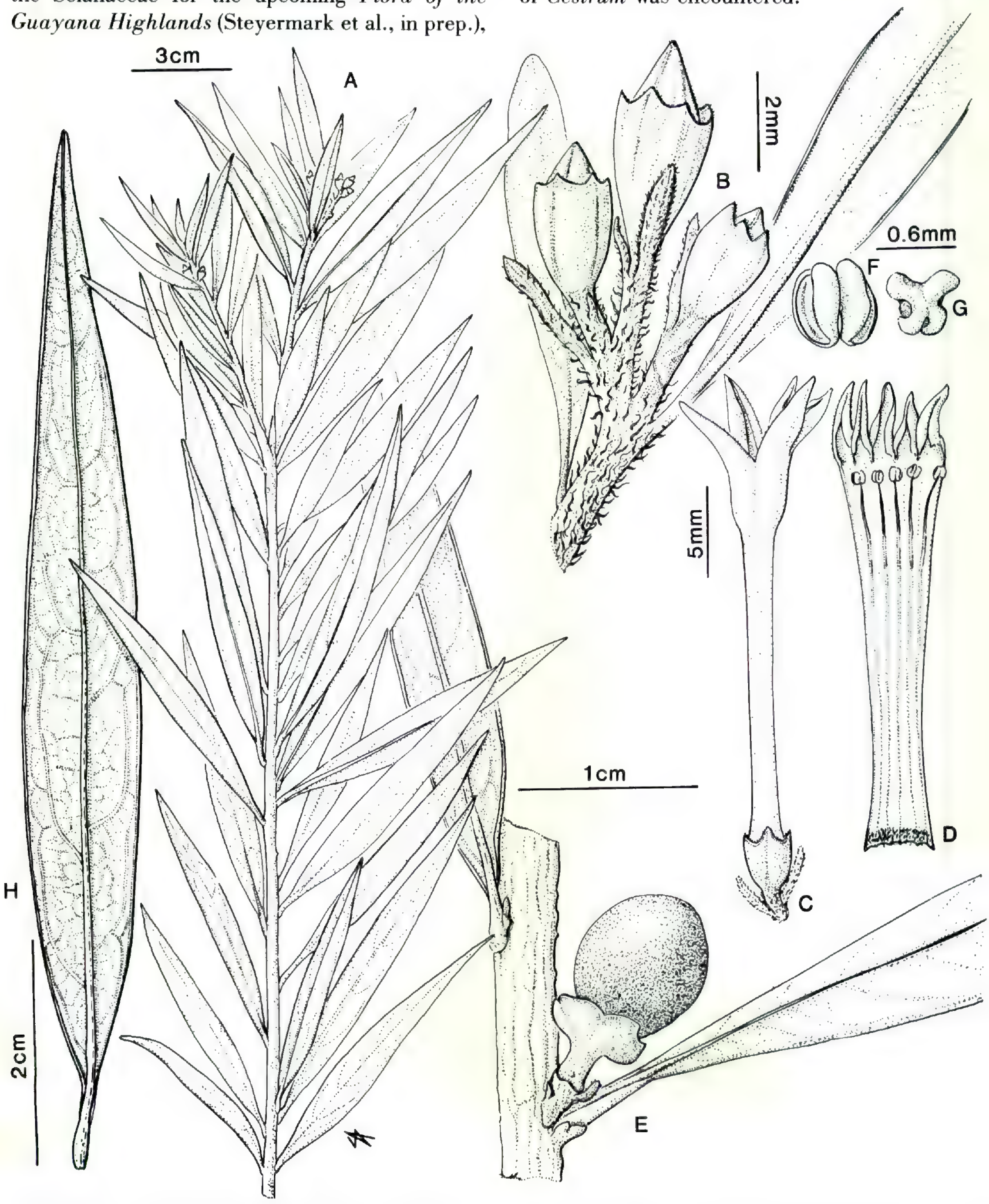

FIGURE 1. *Cestrum neblinense* (*Liesner 16661*).—A. Branch with flower buds.—B. Young inflorescence.—C. Flower.—D. Opened corolla.—E. Fruit.—F, G. Anthers.—H. Leaf, abaxial side.

Cestrum neblinense, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro de La Neblina, 0°51′N, 65°57′W, 700 m, Mar. 1984, *Liesner 16661* (holotype, MO).

Frutex 1–2 m altus, ramis rufo-tomentosis, pilis curvis, ascendentibus, multicellularibus. Folia solitaria, anguste lanceolata, apice acuminato, parce pilifera. Flos calyce glabrato, 2.5 mm longo, bulboso; corolla 27 mm longa, extus et intus glabra praeter partem imum tomentosum; staminibus subaequilongis, rectis, edentatis, glabris, antheris inclusis.

Shrub 1–2 m tall; twigs reddish, tomentulose with curved, ascending, multicellular hairs, older branches glabrate, longitudinally furrowed and minutely tuberculate from the bases of the caducous trichomes; bumpy from the nodes (bases) of fallen leaves. Leaves narrowly lanceolate, sometimes slightly oblique, subcoriaceous or stiffly papyraceous, mostly 8–10 cm long, 10–11 mm wide, apically narrowly acute or acuminate, basally acute or obtuse, drying slightly discolorous, shiny above, glabrescent above except sometimes near the midvein and sometimes glabrescent beneath, the midvein greatly elevated above and beneath, the lateral venation of 4–6 prominent and conspicuous, looping, brochidodromous veins on each side of the midvein, the lateral veins lighter-colored beneath, the minor venation evident, the margins slightly revolute, both sides of margins puberulent with scattered curved whitish hairs; petioles 2–4 mm long, indistinct from the blade. Minor leaves wanting. Inflorescences 1–3-flowered clusters on axillary short-shoots or terminal; rachis tomentulose, 2–5 mm long; bracts 4–5 mm long; bractlets 2 mm long; pedicels obsolete or up to 1.5 mm long. Flowers with the calyx glabrate, 2.5 mm long, subglobose, indistinctly nerved, undulate-lobed, the lobes ciliolate, 0.3 mm long, the cup basally narrowed into the pedicel; corolla white(?), 27 mm long, the tube slender, slightly expanded in the upper ¼, glabrous outside except for a few hairs in the sinuses near the apex, inside glabrous except for a small tomentose region at the very base, the lobes lanceolate, 2.5 mm long, ciliolate; stamens subequal, ca. 1 mm free, straight, edentate, glabrous, the anthers included, ca. 0.8 mm long. Berry ca. 9 mm long; seeds 7, 5–7 mm long.

Additional specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Río Negro, Cerro de La Neblina, *Maguire et al. 42500* (MO, US).

The willowlike leaves of this species resemble those of *Cestrum salicifolium* Jacq., also from Venezuela, and those of *C. skutchii* Morton from Guatemala, but these species have glabrate twigs, membranaceous or chartaceous leaves, and staminal filaments with dentate appendages. The twigs of *C. neblinense*, with their ascending, curved trichomes, resemble those in *C. tubulosum* Sendt. of southern Venezuela, which in contrast has thick, coriaceous, broadly ovate leaves and stamens with filaments that are free for 6 mm (vs. 1 mm in *C. neblinense*).

This species is named for Cerro de La Neblina, the locality of the type collection.

—William G. D'Arcy, *Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.; and* Carmen Benítez de Rojas, *Facultad Agronomía, Universidad Central de Venezuela, Maracay, Venezuela.*

A NEW *VITEX* (VERBENACEAE) FROM MADAGASCAR

The eastern rainforests remain the least known, and currently most threatened, of the diverse vegetation types of Madagascar. Recent exploration of the forests around the Bay of Antongil, north of Maroantsetra, and on the Masoala Peninsula, the largest remaining tract of eastern rainforest, has yielded the following spectacular new species of *Vitex* L.

Vitex masoalensis G. E. Schatz, sp. nov. TYPE: Madagascar. Toamasina: Masoala Peninsula, 6 hr. walk inland from Antalavia along Antalavia River, 15°46′S, 50°03′E, 450 m, 17 Apr. 1987 (fl, fr), *Schatz & Suzon 1353* (holotype, MO; isotypes, K, MO, P, TAN). Figure 1.

Arbor 7-metralis non ramosa simulans *V. hirsutissima* J. G. Baker, sed foliis epetiolatis, folioliis aequalis, laminis glabrescentibus, foliis consociatis inflorescentis (= bracteae) 3-foliolatis, et corolla alba.

Unbranched tree 7 m tall, 8 cm diam., the bark smooth, gray, the vegetative bud densely ferruginous-hirsute. Leaves restricted to several nodes at the apex, opposite, palmately compound, epetiolate, 5-foliolate; leaflets ± equal, chartaceous, subcoriaceous, somewhat bullate when fresh, obovate, 56–92 cm long, 13–24 cm broad, the apex cuspidate, the base long-attenuate, the margins undulate along basal half, the venation eucamptodromous to weakly brochidodromous with ca. 20 veins per side, the midrib slightly elevated adaxially, prominently elevated abaxially and very stout toward the base, the lateral veins slightly impressed adaxially and elevated abaxially, the upper laminar surface glabrous, minutely foveolate, the midrib sparsely hirsute, the lower surface glabrous, very sparsely puberulous to hirsute along the midrib; petiolule 1–2 cm long, very stout and swollen at the point of attachment. Inflorescence a much-branched, condensed cyme borne in fascicles along the main trunk, i.e., trunciflorous, sometimes associated with foliaceous bracts; bracts 3-foliolate, the leaflets ± equal, chartaceous, subcoriaceous, sessile, narrowly elliptic to oblanceolate, 29–33 cm long, 3.5–6 cm broad, the apex long-acuminate to cuspidate, the base attenuate, the margins entire, the venation eucamptodromous to weakly brochidodromous with ca. 11 lateral veins per side, the midrib impressed adaxially, prominently elevated abaxially, the upper laminar surface glabrous, the midrib sparsely hirsute, the lower surface very sparsely appressed pubescent, essentially glabrous; pedicel slender, 0.5–0.8 cm long, densely ferruginous hirsute, bearing 1–several densely ferruginous-hirsute, linear to filiform bracteoles; calyx campanulate, 0.5 cm long and broad, the 5 lobes apiculate, 0.4 cm long, densely ferruginous-hirsute; corolla zygomorphic, short-tubular, 1.5–1.8 cm long, 0.2–0.3 cm broad at the base, to 1.2 cm broad at the apex, white, fading to pinkish white, with longitudinal venation evident, the upper 2 and central 2 lobes triangular, 0.7 cm long, 0.6 cm broad, the apex acute, the margin entire, the lower lobe (lip) narrowly elliptic, 1.2 cm long, 0.5 cm broad, the apex rounded, the margin crenulate, all the lobes ferruginous-hirsute outside, glabrous inside; stamens 4, adnate to the corolla 0.7 cm from the base, the filaments 2.5 cm long, white, basally hirsute for 0.6–0.7 cm, the trichomes to 0.2 cm long, the anthers 0.2 cm long, pink fading to gray-blue, 2-celled; style 2–3 cm long, white, the stigma bifid, the branches 0.3 cm long. Calyx accrescent in fruit, cotyliform, enclosing ½ of the fruit. Fruit a drupe, globose, 0.8 cm diam., pink turning to purple, the exocarp glossy, the mesocarp thin, somewhat fleshy, the endocarp hard.

With over 40 endemic species, Madagascar represents an important center of radiation for the genus *Vitex* (Moldenke, 1956). *Vitex masoalensis* is undoubtedly most closely related to *V. hirsutissima* J. G. Baker, also known from the Masoala Peninsula, with which the former shares a similar monocaulous habit and trunciflorous inflorescences. From *V. hirsutissima*, the new species differs in having sessile leaves with the leaflets all more or less equal. In addition, the lamina is soon glabrescent, lacking the persistent hirsute pubescence characteristic of *V. hirsutissima*. The large, foliaceous bracts sometimes associated with inflorescences are three-foliolate in *V. masoalensis* versus one-foliolate in *V. hirsutissima*.

Special thanks are due to John Myers for the excellent illustration and to Gerrit Davidse for comments on the manuscript.

FIGURE 1. *Vitex masoalensis* (*Schatz & Suzon 1353*).—A. Flower.—B. Fruit.—C. Adaxial surface of leaf.—D. Abaxial surface of leaf showing swollen petiolules, and detail of venation.—E. Foliaceous bract associated with an inflorescence.—F. Habit.

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A NEW SPECIES OF *MACROLOBIUM* (FABACEAE: CAESALPINIOIDEAE) FROM MESOAMERICA

In the course of botanical exploration in the region of Cerro Coronel in northeastern Costa Rica in 1986 and 1987, botanists from the Missouri Botanical Garden and the Museo Nacional de Costa Rica made many collections from this isolated group of low rolling hills. Two species of *Macrolobium* were collected, *M. costaricense* W. Burger and an undescribed and closely related one which is here named in honor of Gerardo Herrera, an astute and energetic Costa Rican botanist and co-collector of the type gathering.

In the last revision of the genus *Macrolobium* (Caesalpinioideae–Amherstieae) Cowan (1953) recognized 48 species. Since then, 22 additional species have been added, 19 of them by Cowan, the majority from previously unexplored areas of Venezuelan Guayana (TROPICOS, 1989). *Macrolobium* is considered to be wholly neotropical, the African taxa previously considered as part of the genus having been relegated mostly to the African genera *Gilbertiodendron* and *Anthonotha* by J. Léonard (see Cowan & Polhill, 1981). Of the 25 genera recognized for the tribe Amherstieae, only *Macrolobium* and *Dicymbe* are native to the New World.

Although not a single Costa Rican specimen of *Macrolobium* was known to Cowan in 1953, two species from that country have since been described by Burger (1968) and Cowan (1985), *M. costaricense* and *M. hartshornii*, respectively. Both of these species, as well as the new taxon described herein, are members of sect. *Stenosolen* Harms and have leaves with few to many pairs of leaflets. Other closely related species are *M. trinitense* Urban from Trinidad, *M. stenosiphon* Harms of Pacific coastal Colombia and adjacent Ecuador, and *M. colombianum* (Britton & Killip) Killip, with six varieties, in northwestern South America and Panama.

Macrolobium herrerae Zarucchi, sp. nov. TYPE: Costa Rica. Limón: hills 2 airline km SSE of Islas Buena Vista in the Río Colorado, 14 airline km SW of Barra del Colorado, premontane wet forest on low hills, 10°40′N, 83°40′W, 10–120 m, 13–14 Sep. 1986 (fl), *Gerrit Davidse & Gerardo Herrera 31126* (holotype, MO; isotypes, AAU, CR n.v., F, K, MEXU, NY, US). Figure 1.

Species *Macrolobio costaricensi* W. Burger et *M. hartshornii* Cowan similis, sed foliolis plerumque 6–7-jugis, foliolis distalibus iis jugorum medianorum haud majoribus, hypanthio parvo, et gynoecio dense tomentoso abstans.

Small or medium-sized tree to 25 m. Branchlets dark purplish, essentially glabrous, sparingly lenticellate. Stipules absent or possibly early caducous. Leaves 8.5–12(–15) cm long with (5–)6–7 pairs of leaflets, petiole (3–)5–12 mm long with the rachis not extending past the terminal pair of leaflets; rachis narrowly winged with the upper surface flat or slightly canaliculate, sparingly pubescent; leaflets sessile to subsessile, 5–7(–8) × 1.4–2(–2.3) cm, elliptic and generally becoming falcate, moderately to strongly inequilateral at the base, apex acuminate and ultimately retuse, both surfaces glabrous except for the sparingly tomentose midrib above; midvein of leaflets slightly impressed above, prominent below, secondary venation discernible on both surfaces. Inflorescences axillary, generally on older branches at leafless nodes or where older leaves persist, racemose, dense; axis 5–10(–15) mm long, often several to many inflorescences densely clustered; pedicels 3–4 mm long, finely pubescent. Bracteoles ca. 4 mm long, connate for ½–⅔ of their length, splitting and persistent through early fruit development. Flowers with the hypanthium cylindric, 3–4 mm long, ca. 1 mm in diameter, glabrous, the stipe 1–2 mm long; sepals 4, elliptic to elliptic-oblong, 4–5 × 1.5–2 mm, unequal with the dorsal one wider than the rest, glabrous; single petal obovate, undulate, 13–16 × 7–8 mm, basally obtuse, apically rounded, glabrous, white with yellow lines; stamens 3, the filaments 13–15 mm long, villosulose along the basal third, purple; anthers versatile, ca. 1.5 mm long; gynoecium slightly sigmoid; ovary ca. 3 × 1 mm, very densely tomentose; gynophore 2–3 mm long; style 9–12 mm long, very thin, terete; stigma capitellate. Fruit 8–10 × 2.5–3.3 cm, narrowly elliptic-oblong or slightly obovate, glabrous, the margins slightly thickened, attached obliquely

FIGURE 1. *Macrolobium herrerae*.—A. Habit.—B. Inflorescence.—C. Flower.—D. Gynoecia.—E. Fruit. (A–D after *Davidse & Herrera 31126*, E after *Alduvín 160*).

at the rounded base to a stipe 5–7 mm long, the acumen 1.5–3 mm long. Seeds 2–4 per fruit, oval, flattened, immature.

Paratypes. HONDURAS. ATLÁNTIDA: Aldea El Pino a 10 km de La Ceiba, faldas del Cerro Pico Bonito, 2 Apr. 1977 (fr), *Carolina Alduvín 160* (MO, ?TEFH n.v.). COSTA RICA. LIMÓN: Cerro Coronel, E of Río Zapote, along and above new road within 1 km of Río Colorado, tall evergreen forest and edge of *Raphia* swamp on gentle to moderate slopes, 10°40′N, 83°40′W, 10–40 m, 13–14 Sep. 1986 (fl), *W. D. Stevens & O. M. Montiel 24327* (CR n.v., F, MEXU, MO).

This new species is apparently most closely related to *Macrolobium costaricense*, also collected in the vicinity of Cerro Coronel, and additionally known from Panama and the Department of Antioquia in Colombia. The single available fruiting collection of *M. herrerae* (*Alduvín 160*) is the northernmost record (ca. 16°N) for the genus. The new species is best distinguished from *M. costaricense* by having a densely tomentose ovary and more numerous pairs ([5–]6–7) of leaflets with the distal pair more or less equal in size to those attached lower on the rachis. In *M. costaricense* the terminal pair of leaflets is larger. Also, the fruit of *M. costaricense* has valves markedly broader toward the apex, whereas the valves in *M. herrerae* may be only slightly wider distally. *Macrolobium herrerae* differs from all varieties of *M. colombianum* by the densely tomentose ovary and generally smaller floral parts, especially the hypanthium.

Since *Macrolobium herrerae* was collected along the Costa Rica–Nicaragua border in tropical wet, evergreen forest and is also known from Honduras, it probably occurs in Nicaragua.

I thank John Myers for the excellent illustration, and Gerrit Davidse, John Dwyer, Rupert Barneby, and W. Douglas Stevens for comments on the manuscript. Botanical exploration in Costa Rica by Stevens, Montiel, and Davidse, all of the Missouri Botanical Garden, was supported by the National Geographic Society Grant #2785-84.

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A NEW SPECIES AND NEW COMBINATION IN *CAMPYLONEURUM* C. PRESL (POLYPODIACEAE)

During a taxonomic revision of the neotropical fern genus *Campyloneurum* C. Presl, I found that a new combination and new species name are needed for two South American taxa.

Campyloneurum nitidissimum (Mett.) Ching var. **abruptum** (Lindman) B. León, comb. nov. *Polypodium repens* Aublet var. *abruptum* Lindman, Ark. Bot. 1: 245. 1903. TYPE: Brazil. Matto Grosso: Serra do Itapirapuam, ad arbores, 28 Apr. 1894, *Lindman (Regnell Exped. I) 3345* (lectotype, here designated, S; isolectotype, K). Figure 1A, B, C.

Polypodium nitidissimum Mett. var. *latior* Rosenstock, Repert. Spec. Nov. Regni Veg. 12: 474. 1913. TYPE: Bolivia. La Paz: Yungas septentrionalis, Polo Polo, prope Coroico, 900 m, *Buchtien 3526* (holotype, S; isotypes, F, US).

Campyloneurum nitidissimum var. *abruptum* occurs from Venezuela and Colombia to Bolivia and Brazil, usually at 100–1,500(2,000) m. It grows terrestrially on slopes of rock, sand, or clay, at the base of trees, and rarely as a hemiepiphyte in lower montane or lowland forests. It is usually misidentified in herbaria as *C. coarctatum* (Kunze) Fée, from which it differs by its narrow, long-creeping stem, widely spaced phyllopodia, and leaves less than 40 cm long.

Campyloneurum nitidissimum is characterized by its dark brown, linear scales, and stem 5–10 mm wide. *Campyloneurum nitidissimum* var. *nitidissimum* generally has asymmetrically divided primary areoles and two to three sori between secondary veins, and always has subcoriaceous leaves. *Campyloneurum nitidissimum* var. *abruptum* differs from the typical variety by having undivided primary areoles, two sori between secondary veins, and herbaceous-chartaceous leaves.

Selected specimens examined. VENEZUELA. MERIDA: ESE of Santa Bárbara, 7°41′N, 71°28′W, 9 Mar. 1980, *Liesner & González 9236* (MO). TÁCHIRA: W of Pinal, W of bridge over Río Frío, 27–30 Aug. 1966, *Steyermark & Rabe 96710* (GH). BARINAS: Pedraza, above El Algarrobo, 8°31′N, 70°35′W, 3 Aug. 1983, *Werff & Ortiz 5810* (UC). COLOMBIA. BOLÍVAR: Boca Verde, on Río Sinú, 13–14 Feb. 1918, *Pennell 4216* (NY). SUR DE SANTANDER: vicinity of Barranca Bermeja, Magdalena valley, between Sogamoso and Colorado rivers, 19 Feb. 1935, *Haught 1567* (US). BOYACA: Casanare, Tauramena, bosques del Río Caja, 13 Apr. 1963, *Uribe 4281* (US). TOLIMA: Alto de Consuelo, Honda, July 1923, *Ariste 4997* (F, GH). HUILA: 10 km SSW (by road) of La Plata, on road to Purace, 29 Apr. 1972, *Duncan 1889* (UC). ECUADOR. PICHINCHA: between Nono and Nanegal, 14 km NW of Nono, 4 Sep. 1976, *Croat 38838* (UC). NAPO: Río Wai Si Aya, a northern tributary to Río Aguarico, 8 Aug. 1980, *Brandbyge et al. 32661* (AAU). PASTAZA: Río Bufeo, northern tributary of Río Bobonaza, 2°20′S, 76°40′W, 19 July 1980, *Ollgaard et al. 34779* (AAU). PERU. SAN MARTÍN: Chazuta, Río Huallaga, Apr. 1935, *Klug 4080* (F, GH, S, UC, US). HUANUCO: Huánuco, near confluence of Río Cayumba with Río Huallaga, 10 Oct. 1936, *Mexia 8272* (BM, F, GH, S, UC). PASCO: Oxapampa, Quebrada Honda, camino a Tunqui, 17 Aug. 1985, *León 667* (GH, USM). JUNÍN: camino a Tarma, antes de Carpapata, 1 Oct. 1982, *León 340* (GH, USM). MADRE DE DIOS: Tambopata, lodge "Cuzco Amazónico," Apr. 1986, *León 884* (USM). BOLIVIA. LA PAZ: Larecaja, between Caranavi and Guanay, 15°33′S, 67°45′W, 28 Nov. 1980, *Croat 51658* (MO, UC); Nor Yungas, 4.5 km below Yolosa, 16°12′S, 67°50′W, 19–20 Oct. 1982, *Solomon 8549* (MO); Tumupasa, 22 Jan. 1912, *R. S. Williams 1059* (GH, NY). TARIJA: Arce, vic. Comunidad Sidras, 22°14′S, 64°32′W, 6 May 1983, *Solomon 10535* (NY, UC). BRAZIL. RORAIMA: Posto Mucajaí, Rio Mucajaí, vic. Mucajaí airstrip, 13 Mar. 1971, *Prance et al. 10923* (K, NY, S, US). AMAZONAS: Rio Curuquete, Cachoeira República, 25 July 1971, *Prance et al. 14584* (NY, US). PARÁ: W bank of Rio Maicuru, ca. 23 km from Lageira, 0°55′S, 54°26′N, 29 July 1981, *Strudwick et al. 3702* (NY). RODÔNIA: basin of Rio Madeira, 2 km below confluence of Rio Abunã, 12 Nov. 1968, *Prance et al. 8341* (S, US). MATO GROSSO: Mato do Curupira, 18 Feb. 1894, *Lindman (Regnell Exped. I) 3075* (S); gorge of Veu de Noiva, Chapada dos Guimaraes, 17 Oct. 1973, *Prance et al. 19105* (US). GOÍAS: Yateri, Balsamo, 9 Feb. 1895, *Macedo 5298* (S, US). MINAS GERAIS: Rio Branco, 13 Nov. 1930, *Mexia 5298* (BM, NY, S).

Campyloneurum wurdackii B. León, sp. nov. TYPE: Venezuela. Bolívar: Cerro Pijiguao, Sierra Suapuré, 400–450 m, 19 Jan. 1956, *Wurdack & Monachino 41303* (holotype, MO; isotype, US). Figure 1D, E, F.

Differt haec species a *Campyloneurum repens* 3–4 venulis excurrentibus in quaque areola. Mediae venulae excurrentes venulis transversalibus junctae sunt, formantes areolas secundarias. Haec species differt ab *C. nitidissimum* paleis lanceolatis, 3–4 mm longis.

Terrestrial. Stem long-creeping, not pruinose, 2–3 mm diam.; scales light brown, lanceolate, 3–

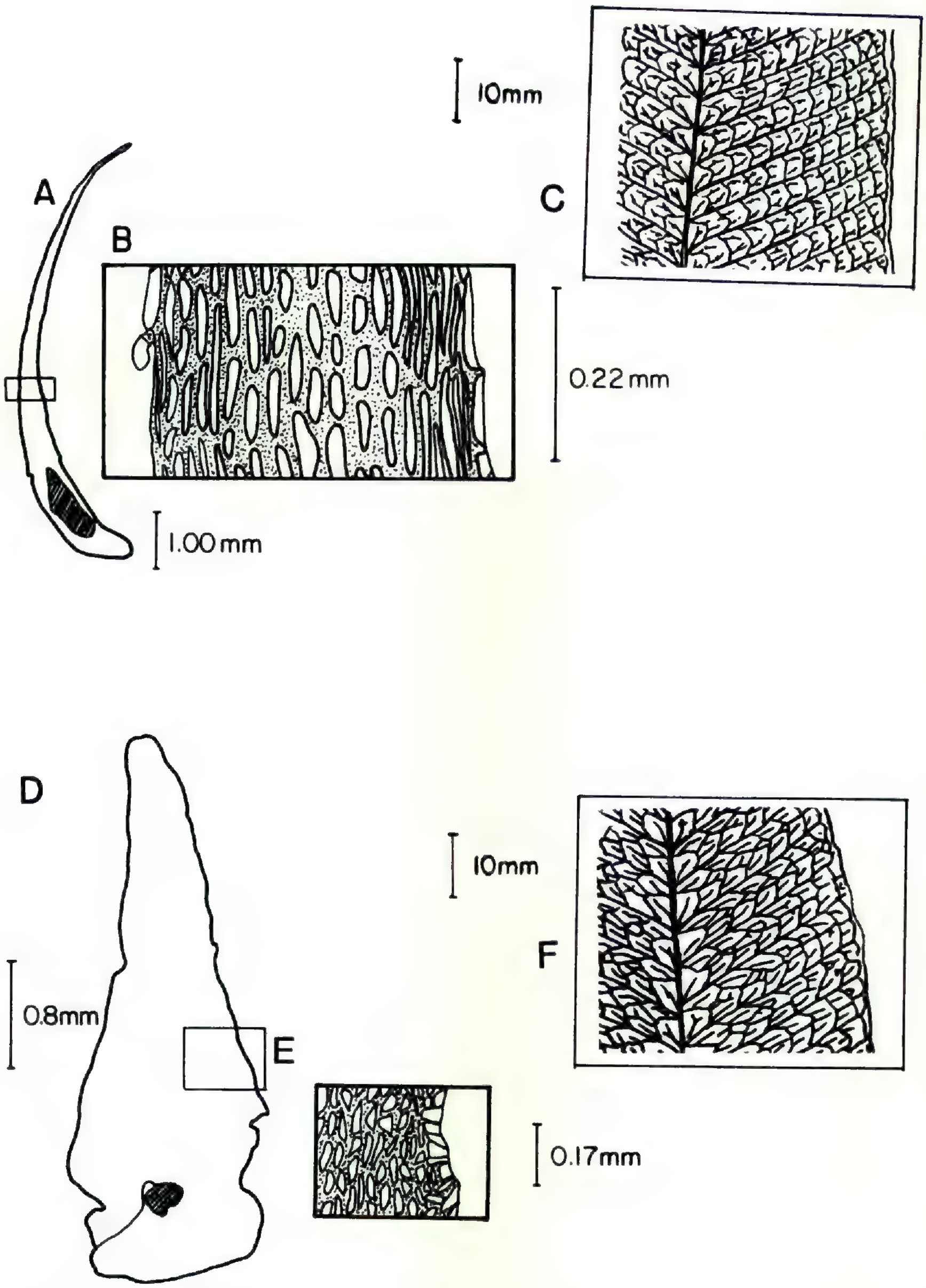

FIGURE 1. A–C. *Campyloneurum nitidissimum* var. *abruptum*.—A. Stem scale (100×).—B. Cell structure from the middle part of the stem scale (100×) (A–B, *Mexia 8272* F).—C. Detail of venation pattern (1×) (*Karsten s.n.* W). D–F. *Campyloneurum wurdackii* (*Wurdack & Monachino 41303* MO).—D. Stem scale.—E. Cell structure from middle part of the stem scale (100×).—F. Detail of the venation pattern (1×). (Hatched area on both scales represents the insertion zone.)

4 mm long, 1–1.3 mm wide, with bases auriculate, apices obtuse or rarely acute; phyllopodia 5 mm apart. Leaves 19–41 cm long; petiole 4–8 cm long, stramineous. Lamina simple, lanceolate, with bases cuneate then long decurrent, apices acuminate to slightly caudate. Veins prominent or prominulous, secondary veins straight, 60–65° divergent from the costa, tertiary veins forming 7–8 primary areoles between the costa and margin, excurrent veinlets 3–4 per areole, simple or furcate, central veinlet generally anastomosed with the transverse vein forming asymmetric secondary areoles. Sori subterminal or medial, rarely basal, on the free excurrent vein; paraphyses absent.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Atures, 23 km NE of Puerto Ayacucho, near Cachama, 5°51′N, 67°24′W, 17–19 Apr. 1978, *Davidse & Huber 15306* (MO).

Campyloneurum wurdackii is known only from Venezuela, where it has been collected twice from mossy places in lowland forests at 90–500 m.

Campyloneurum wurdackii and *C. nitidissimum* var. *abruptum* have similar cuneate leaf bases that are decurrent on the petiole. However, the former species has a stem 2–3 mm wide, lanceolate scales, and venation with divided primary areoles (Fig. 1D–F), while the latter has a stem 5–10 mm wide, linear scales, and venation with usually undivided primary areoles (Fig. 1A–C).

Campyloneurum wurdackii appears to be closely related to *C. brevifolium*, as both species have asymmetrically divided areoles, approximate leaves, and slightly clathrate stem scales. However, the former has a stem 2–3 mm wide and lanceolate stem scales, whereas the latter has a stem 5–10 mm wide and ovate-lanceolate stem scales.

Vareschi (Fl. Venez. 1(2): 950. 1969) previously named *Campyloneurum wurdackii* as *Polypodium repens* Aublet var. *spathulatum* Vareschi a nomen nudum because it lacked a Latin description. He cited *Wurdack 41130* as the type of his new variety, but this number represents an angiosperm (J. Kalluncki, pers. comm.). The number *41130* undoubtedly is a typographic error for *Wurdack 41303*, a specimen of *Campyloneurum* that corresponds to the description of his new variety and from the same locality cited by Vareschi. The name honors Dr. J. J. Wurdack, who collected the type.

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A NEW SPECIES OF *PALICOUREA* (RUBIACEAE) FROM COSTA RICA

Palicourea Aublet is a genus of about 200 species of shrubs and small trees found throughout the moist and wet Neotropics, with 24 species presently known from Costa Rica, including this new one. The recent treatment of *Palicourea* in Central America (Taylor, 1989) does not include this species.

Palicourea gomezii C. M. Taylor, sp. nov. TYPE: Costa Rica. Heredia: quebrada Sangrijuela, 700 m, flower & fruit, *Gómez, Chacón & Herrera 20896* (holotype, CR; isotype, MO). Figure 1.

Frutex 2–5 m altus, pilosulus. Folia petiolata; laminis ellipticis, 11–20.5 cm long. × 5–9 cm lat., chartaceis, paribus 11–15 venarum secundariarum munitis; stipularum foliacearum laminis interpetiolaribus 8–12 mm longis bilobatis ad partem quartam longitudinis divisis, lobis ovatis. Inflorescentia subsessilis, ex thyrso oblato ramis inferioribus elongatis constans, viridis, 4–4.5 cm long. × 6–8 cm lat.; bracteis 0.5–7 mm longis; pedicellis 1.5–5 mm longis; florum lobis calycinis 1–3 mm longis, in eodem flore inaequalibus; corolla infundibulari basi valde gibbosa, alba colore roseo suffusa, externe glabra, tubo 7 mm longo, lobis 3–5 mm longis. Fructus obovoideus, 6 mm longus.

Succulent shrubs or small trees to 5 m tall, sparsely to densely pilose to pilosulous, sometimes becoming glabrescent in older parts. *Leaves* with *blades* elliptic, at apex acute to acuminate with the tip 0.5–1 cm long, at base acute to cuneate, 11.5–20 cm long, 5–9 cm wide, about 2.2–2.3 times as long as wide, chartaceous, secondary veins 11–15 on each side of costa, widely angled with the costa, widely curving, not looping to connect, with 1(–2) well-marked intersecondary veins present between each pair of secondary veins, margins not revolute; *petioles* 1–5 cm long; *stipules* forming ovate interpetiolar laminae, 8–12 mm long, at apex broadly rounded and emarginate, the sinus between the lobes about 1–3 mm deep. *Inflorescences* rounded to somewhat pyramidal, 4–4.5 cm long, 6–8 cm broad, about 0.5–0.6 times as long as broad at base, peduncles 0–0.5 cm long (the panicle often appearing tripartite), not geniculate at base, bracts triangular to lanceolate, 0.5–7 mm long, those subtending primary branches about 5–7 mm long and those subtending pedicels about 0.5 mm long; pedicels 1.5–5 mm long; peduncle, branches, bracts, and pedicels green, glabrescent. *Flowers* with *calyx* green, glabrescent, the free portion divided to base, lobes triangular to lingulate, acute, 1–3 mm long and strongly unequal in length on an individual flower; *corolla* carnose, funnelform, swollen and strongly gibbous at base, the tube curved at ca. 90° just above the swelling, lilac to rose or white flushed with these colors, externally glabrous, internally glabrous except for a ring ca. 5 mm wide of trichomes just above the basal swelling and extending to the stamen insertion, tube 7 mm long, lobes triangular to lingulate, acute, 3–5 mm long; *anthers* in short-styled flowers 4 mm long; *styles* in short-styled flowers ca. 5 mm long, stigmas 1 mm long. *Infructescences* similar in size and proportion to inflorescences; immature *fruit* obovoid, flattened, 6 mm long; well-developed *pyrenes* not seen.

This new species is distinguished by emarginate laminar stipules with rounded lobes; subsessile or sessile, relatively broad inflorescences; relatively long calyces with unequal lobes 1–3 mm long; and strongly gibbous rose or lilac (or white flushed with these colors) corollas with proportionately long lobes, half or more the length of the corolla tube. Among Central American plants the new species can be confused with *Psychotria copensis* Dwyer from Panama, which is probably better placed in *Palicourea* (Taylor, in prep.). The Panamanian species differs in its usually more numerous secondary leaf veins, (13–)15–24 rather than 11–15; acute rather than rounded stipule lobes; and blue corollas with proportionately shorter lobes, a third or less the length of the tube. *Palicourea gomezii* also resembles an undescribed species from Panama (Taylor, in prep.), which differs in its more contracted inflorescences 2–2.5 cm long by 3–4 cm broad in contrast to 4–4.5 cm long by 6–8 cm broad in *P. gomezii*; pedicels 1–2 mm long in contrast to 1.5–5 mm long in *P. gomezii*; acute stipule lobes; three-veined calyx lobes in contrast to lobes with no evident venation in *P. gomezii*; and farinaceous corollas in contrast to the glabrous corollas of *P. gomezii*.

The epithet honors Sr. Luis Diego Gómez P.,

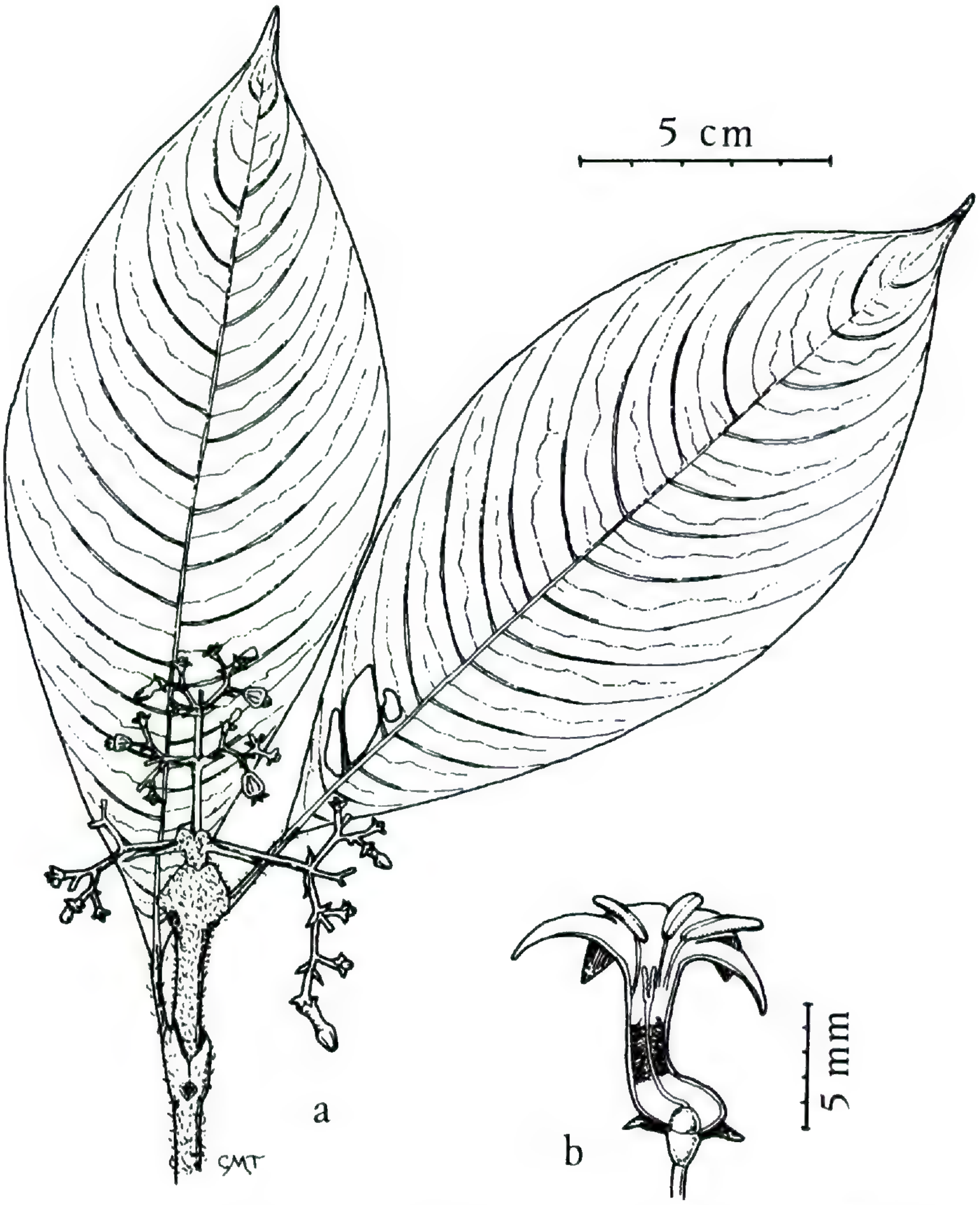

FIGURE 1. *Palicourea gomezii* (*Gómez et al. 20896* MO).—a. Inflorescence and node with leaves.—b. Flower, partial longitudinal section.

Director of the Museo Nacional of Costa Rica during a long and productive period.

All flowers examined resemble the short-styled morph of distylous species of *Palicourea*. Relatively few specimens have been seen, however, so this species may be distylous. All the collections seen were collected in January or March and are simultaneously flowering and fruiting.

Paratypes. COSTA RICA. HEREDIA: Ríos Sucio y Hondura, Parque Braulio Carillo, 500 m, *Gómez-Laurito 6401* (CR); 13 km en la carretera a Guapiles, 800 m, *Gómez-Laurito 6423* (CR); 11 km E of Cariblanco, 10°16′N, 84°05′W, 1,060 m, *Loiselle 258* (MO).

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NOTES ON THE FLORAL MORPHOLOGY AND ECOLOGY OF *MARGARITARIA DISCOIDEA* (EUPHORBIACEAE) AT MUFINDI, TANZANIA

Margaritaria discoidea (Baillon) Webster is a common and widespread African tree found in deciduous woodland, fringing forest, dry evergreen forest, rainforest, and disturbed vegetation at altitudes from near sea level to over 2,000 m (Radcliffe-Smith, 1987). At Ngwazi, Mufindi District, Iringa Region, Tanzania (08°31′S, 35°10′E, altitude 1,850 m, rainfall 850 mm/year, mean monthly temperature from 17.5°C in January to 13.5°C in June with occasional frosts) *M. discoidea* var. *nitida* (Pax) R.-Sm. occurs as a tree 5 m tall in tree clumps associated with termite mounds in grassland. This variety also grows at the edges of planted wattle breaks (*Acacia mearnsii* De Wild., Leguminosae: Mimosoideae) and flowers in mid-October at the end of the dry season but before the start of the rains, which are initially short, heavy thunderstorms. The flowers are produced before and during a flush of leaves, and before the stipules fall. Old leaves can persist until just before the new leaf flush. The trees are generally dioecious, although one individual was seen with female flowers on a predominantly male tree (*Lovett 3248*, DSM, K, MO). Armstrong & Irvine (1989) observed a similar occurrence in the dioecious *Myristica insipida* R. Br. (Myristicaceae) of Queensland, Australia.

The Flora of Tropical East Africa (Radcliffe-Smith, 1987), followed taxonomically here, and Webster (1979) described *Margaritaria* as having four sepals and four stamens. However, in a sample of 1,000 flowers from a female tree (*Lovett 3251*, DSM, K, MO), 657 flowers had four sepals, 326 had five sepals, and 17 had six sepals. In a sample of 1,000 flowers from a male tree (*Lovett 3247*, DSM, K, MO), 8 had two stamens, 37 had three stamens, 926 had four stamens, and 29 had five stamens. On another tree a flower with six stamens was also seen. In male flowers the sepals are reflexed in a square, so are not as visible and easy to count as the sepals on female flowers. Female flowers were visited by ants and honey bees (*Apis mellifera*), which are kept at Ngwazi for honey production.

Associated species in the tree clumps include the trees: **Albizia gummifera* (J. Gmelin) C. A. Smith var. *gummifera* (Leguminosae: Mimosoideae), **Apodytes dimidiata* Arn. var. *dimidiata* (Icacinaceae), *Bequaertiodendron magalismontanum* (Sonder) Heine & J. Hemsley (Sapotaceae), **Bersama abyssinica* Fresen. subsp. *abyssinica* var. *abyssinica* (Melianthaceae), *Buddleja salvifolia* (L.) Lam. (Loganiaceae), *Canthium lactescens* Hiern (Rubiaceae), *Carissa edulis* Vahl (Apocynaceae), **Cassipourea malosana* (Baker) Alston (Rhizophoraceae), **Catha edulis* (Vahl) Forsskal ex Endl. (Celastraceae), *Croton macrostachyus* Del. (Euphorbiaceae), *Cussonia arborea* Hochst. ex A. Rich. (Araliaceae), **Cussonia spicata* Thunb. (Araliaceae), *Dais cotinifolia* L. (Thymelaeaceae), **Diospyros whyteana* (Hiern) F. White (Ebenaceae), *Dombeya rotundifolia* Harvey (Sterculiaceae), **Ekebergia capensis* Sparrman (Meliaceae), *Erythrina abyssinica* Lam. ex DC. subsp. *abyssinica* (Leguminosae: Papilionoideae), *Erythrina lysistemon* Hutch. (Leguminosae: Papilionoideae), **Euclea divinorum* Hiern (Ebenaceae), *Flacourtia indica* (Burman f.) Merr. (Flacourtiaceae), **Garcinia kingaensis* Engl. (Clusiaceae), *Heteromorpha arborescens* (Sprengel) Cham. & Schldl. (Apiaceae), *Maytenus* cf. *heterophylla* (Ecklon & Zeyher) N. Robson (Celastraceae), **Olea capensis* L. (Oleaceae), **Olinia rochetiana* Adr. Juss. (Oliniaceae), *Osyris abyssinica* Hochst. (Santalaceae), **Peddiea fischeri* Engl. (Thymelaeaceae), **Prunus africana* (Hook.f.) Kalkman (Rosaceae), **Psychotria mahonii* C. H. Wright var. *puberula* (Petit) Verdc. (Rubiaceae), **Rapanea melanophloeos* (L.) Mez (Myrsinaceae), **Rothmannia fischeri* (Schumann) Bullock (Rubiaceae), **Schrebera alata* (Hochst.) Welw. (Oleaceae), **Syzygium guineense* (Willd.) DC. subsp. *afromontanum* F. White (Myrtaceae), *Tarenna neurophylla* (S. Moore) Bremek. (Rubiaceae), *Tecomaria capensis* (Thunb.) Spach subsp. *nyassae* (Oliver) Brummitt (Bignoniaceae), and **Trichocladus ellipticus* Ecklon & Zeyher subsp. *malosana* (Baker) Verdc. (Hamamelidaceae). Climbers

include: *Asparagus setaceus* (Kunth) Jessop (Liliaceae), *Byrsocarpus orientalis* Baillon (Connaraceae), *Clematis hirsuta* Perrier & Guillaumin (Ranunculaceae), **Dalbergia lactea* Vatke (Leguminosae: Papilionoideae), **Dracaena laxissima* Engl. (Agavaceae), *Jasminum goetzeanum* Gilg (Oleaceae), *Keetia gueinzii* (Sonder) Bridson (Rubiaceae), *Rhus longipes* Engl. var. *longipes* (Anacardiaceae), *Rhoicissus tridentata* (L.f.) Wild & R. Drumm. (Vitaceae), **Rubia cordifolia* L. subsp. *conotricha* (Gand.) Verdc. (Rubiaceae), *Smilax aspera* L. (Smilacaceae), and **Toddalia asiatica* (L.) Lam. (Rutaceae). Shrubs include: **Clausena anisata* (Willd.) Hook.f. ex Benth. (Rutaceae), *Myrsine africana* L. (Myrsinaceae), and **Psychotria zombamontana* (Kuntze) Petit (Rubiaceae).

Flowering at the same time as *Margaritaria discoidea* were *Albizia gummifera, Apodytes dimidiata, Byrsocarpus orientalis, Dombeya rotundifolia, Erythrina abyssinica, Erythrina lysistemon*, and *Rothmannia fischeri*. One kilometer away in *Brachystegia* woodland *Brachystegia spiciformis* Harms (Leguminosae: Caesalpinioideae), *Cussonia arborea*, and *Parinari curatellifolia* Planchon ex Benth. (Chrysobalanaceae) were also flowering. Flowering just before the onset of the rains evidently avoids damage to the flowers by the initial heavy thunderstorms and allows development of fruits through the whole rainy season. Jacaranda trees (*Jacaranda mimosifolia* D. Don, Bignoniaceae) planted at Ngwazi and that flower at the start of the rains failed to set seed in 1986 and 1987 following heavy rains in 1985 and 1986, but did set seed in 1988 following the late and poor rains of 1987. Following a thunderstorm, many flowers from these trees are found knocked to the ground.

Of the associated species, those marked with an asterisk (*) in the above list also occur in the moist forests of the Mufindi escarpment 12 km east of Ngwazi, where the rainfall exceeds 1,600 mm/year. All these species are widespread Afromontane trees. Moist forest species occurring on termite mounds outside their normal climatic range have been observed in Ethiopia (Friis et al., 1987), and it seems likely that termite mounds offer a route whereby moist forest species can disperse across otherwise climatically unsuitable areas.

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SISYMBRIUM LLATASII AND *S. MORRISONII* (BRASSICACEAE), NEW SPECIES FROM COASTAL PERU

The genus *Sisymbrium* L. includes more than 90 species and is most highly diversified in South America, where nearly half of the species grow (Al-Shehbaz, 1988). It was treated on a worldwide basis by Schulz (1924) and has been recently revised for Argentina by Romanczuk (1982). Although several South American species remain to be described, the major taxonomic difficulty in *Sisymbrium* involves generic boundaries. The genus is highly heterogeneous and consists of several lineages of poorly understood phylogenetic interrelationships. Schulz (1924) recognized these lineages as independent genera on the basis of minor morphological differences. I have adopted in this paper and elsewhere (Al-Shehbaz, 1988, 1989) a somewhat broad generic concept of *Sisymbrium*, and I believe that most of Schulz's (1924) South American segregates might not merit recognition.

Sisymbrium llatasii Al-Shehbaz, sp. nov. TYPE: Peru. Lambayeque: Cerro Reque, 580 m, 28 Sep. 1986, *S. Llatas Quiroz 2102* (holotype, F; isotype, GH). Figure 1.

Herba annua glabra, 0.2–0.8 m alta; folia caulina petiolata, oblonga vel lanceolata, obtusa vel subacuta, repanda vel dentata, 2.5–7 cm longa, 0.7–2.5 cm lata; sepala oblonga, patula, 3.5–4 mm longa; petala late obovata, alba vel lilacina, nonunguiculata, apice rotunda, basi cuneata, 6–7 mm longa, 3.5–4 mm lata; pedicelli fructiferi recti, divaricati, 9–13 mm longi; siliquae teretes, anguste lineares, 2.1–3.9 cm longae, 1.7–2 mm latae; styli 0.5–1 mm longi; semina biseriata, oblongo-ovata, 1–1.2 mm longa, 0.8–0.9 mm lata.

Glabrous annual herb. Stems erect, 0.2–0.8 m high, branched above and below. Cauline leaves petiolate, glabrous, oblong to lanceolate, obtuse to subacute at apex, repand to obscurely dentate, cuneate at base, 2.5–7 cm long, 0.7–2.5 cm wide, gradually reduced in size upward; petioles 1–2 cm long. Inflorescences ebracteate, corymbose racemes, elongated and lax in fruit. Sepals oblong, spreading, caducous, glabrous, narrowly scarious at margin, 3.5–4 mm long, 1.7–2 mm wide. Petals white to lavender, dark-veined, broadly obovate, not clawed, rounded at apex, cuneate at base, 6–7 mm long, 3.5–4 mm wide. Stamens slightly tetradynamous; filaments erect, white, 3–3.7 mm long; anthers oblong, sagittate at base, recurved at apex after dehiscence, 0.7–0.9 mm long. Nectar glands well developed, confluent, ringlike, surrounding bases of lateral stamens, subtending those of median ones. Fruiting pedicels divaricate to somewhat ascending, straight, glabrous, slender, much narrower than fruits, 9–13 mm long. Fruits terete, narrowly linear, straight, obscurely torulose, subsessile, 2.1–3.9 cm long, 1.7–2 mm wide; valves glabrous, rounded at both ends, with a conspicuous midvein and obscure lateral veins; style 0.5–1 mm long; stigma slightly 2-lobed; septum hyaline, not veined. Seeds oblong-ovate, orange-brown, coarsely reticulate, biseriately arranged, 1–1.2 mm long, 0.8–0.9 mm wide; cotyledons incumbent.

Additional specimen examined. PERU. LAMBAYEQUE: Chiclayo, Cerro Reque, 540 m, 24 Oct. 1978, *S. llatas [Quiroz] 331* (NY).

Sisymbrium llatasii, which is named after its collector, resembles and perhaps is related to *S. litorale* Philippi, a species endemic to central Chile near Concepción. *Sisymbrium llatasii* is an annual with obscurely dentate to repand leaves, broadly obovate petals, slender fruiting pedicels 9–13 mm long, slender fruits to 2 mm wide, and biseriate, orange-brown seeds 1–1.2 mm long. In contrast, *S. litorale* is a suffruticose perennial with serrulate-denticulate leaves, oblong-spatulate petals, stout fruiting pedicels 2–3 cm long, stout fruits, and uniseriate, dark reddish brown seeds ca. 2 mm long. Both are coastal, narrowly endemic species that are separated from one another by some 3,400 air kilometers.

Sisymbrium morrisonii Al-Shehbaz, sp. nov. TYPE: Peru. Arequipa: 8 km S of Mollendo, silty flat, near sea, base of uplifted conglomerate bench, 28 Sep. 1938, *C. R. Worth & J. L. Morrison 15729* (holotype, UC; photocopy, A). Figure 2.

Herba perennis basi lignosa, pili densis minutis 0.1–0.3 mm longis; folia caulina lanceolata vel ovata, petiolata,

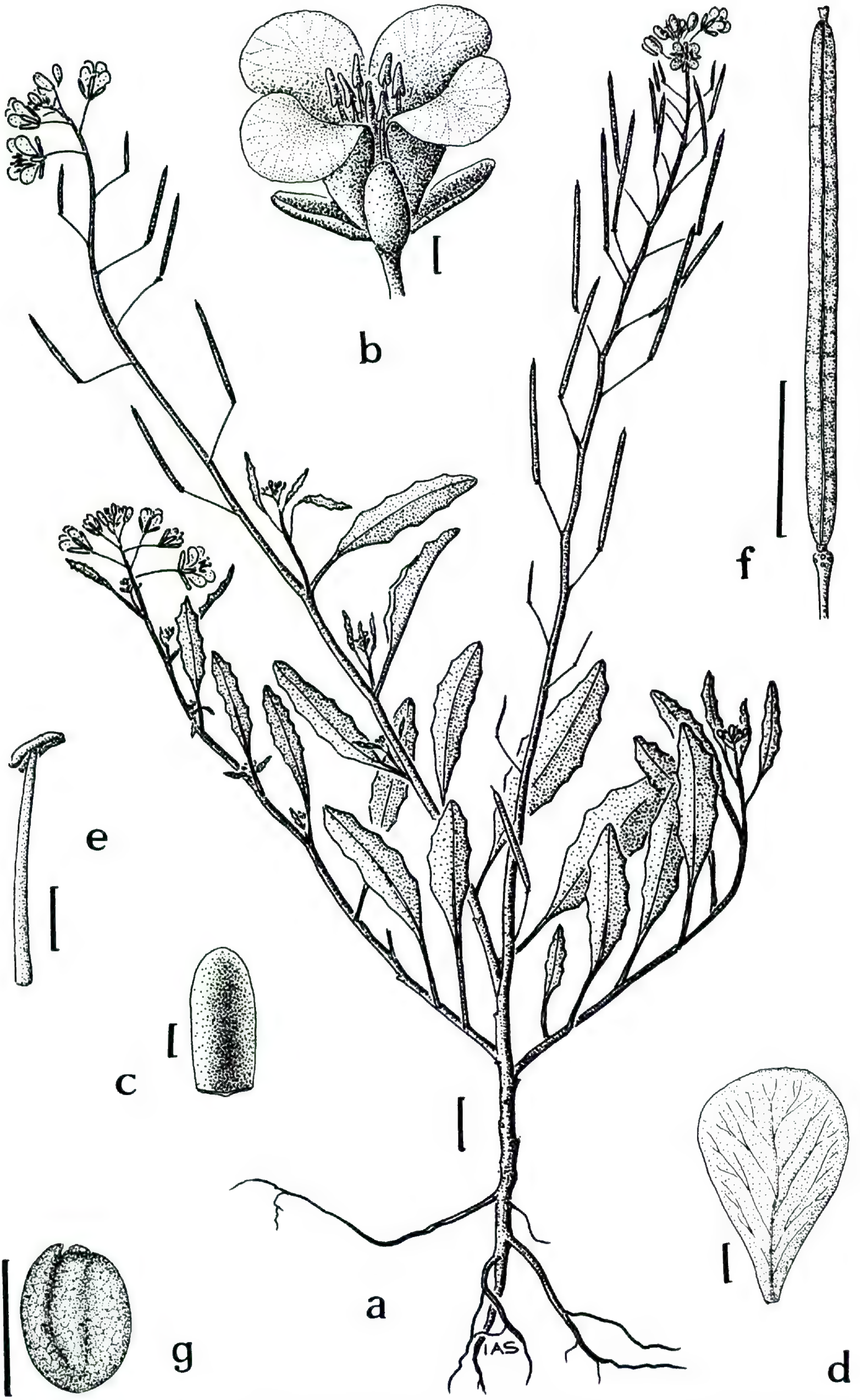

FIGURE 1. *Sisymbrium llatasii*.—a. Plant.—b. Flower.—c. Sepal.—d. Petal.—e. Stamen.—f. Fruit.—g. Seed. Scales a, f = 1 cm; b–e, g = 1 mm. Drawn from the holotype by the author.

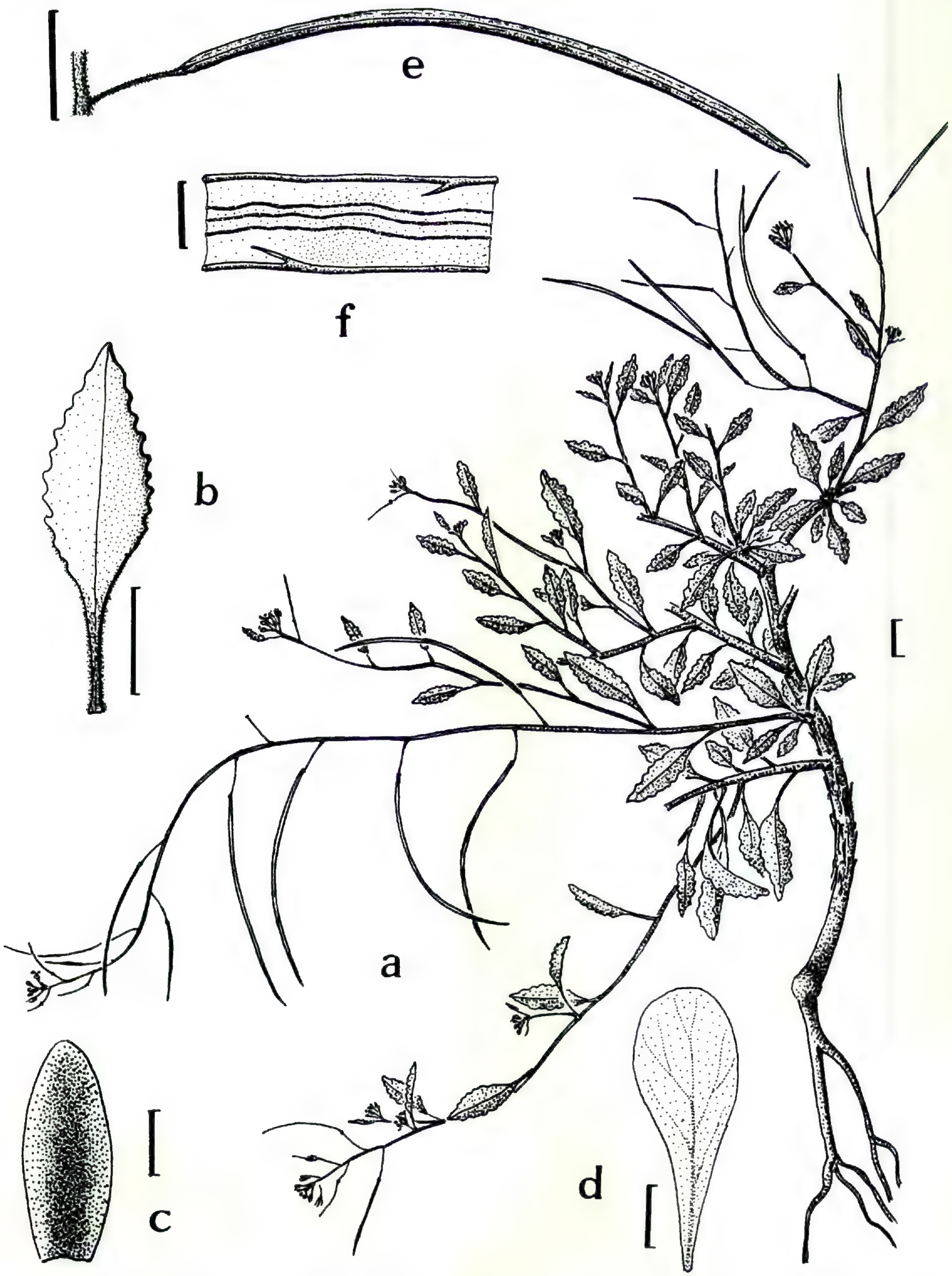

FIGURE 2. *Sisymbrium morrisonii.*—a. Plant.—b. Leaf.—c. Sepal.—d. Petal.—e. Fruit.—f. Portion of replum and septum showing venation. Scales a, b, e = 1 cm; c, d, f = 1 mm. Drawn from the holotype by the author.

dentata vel repanda, cuneata, 2–4 cm longa, 0.5–1.5 cm lata; racemi ebracteati; sepala oblonga, erecta, glabra, 3.5–4 mm longa; petala alba, spathulata, 5–5.5 mm longa; pedicelli fructiferi recti, divaricati, 8–13 mm longi; siliquae teretes, anguste lineares, subfalcatae, glabrae, 5–6.8 cm longae, 1.4–1.6 mm latae; septum trinervum; styli tenues, 1–2 mm longi; semina oblonga, uniseriata, 1.4–1.6 mm longa, 0.9–1 mm lata.

Perennial herb. Stem woody at base, annually producing herbaceous stems 10–25 cm high, densely and minutely pubescent with short, stiff trichomes 0.1–0.3 mm long. Cauline leaves petiolate, ovate to lanceolate, dentate to repand, cuneate at base, subacute at apex, 2–4 cm long, 0.5–1.5 cm wide, reduced in size upward, densely pubescent along the petioles, sparsely so along the midrib and margins, glabrescent on both surfaces. Inflorescences ebracteate, corymbose racemes, elongated considerably in fruit. Sepals oblong, erect, caducous, glabrous, nonsaccate, 3.5–4 mm long, ca. 1.5 mm wide. Petals white, spatulate, narrowed to a clawlike base, 5–5.5 mm long, ca. 1.8 mm wide. Stamens erect, slightly tetradynamous; filaments 3.5–4 mm long; anthers oblong, sagittate at base, ca. 0.8 mm long. Nectar glands confluent, ringlike, subtending the bases of filaments. Fruiting pedicels divaricate, straight, pubescent, slender and much narrower than fruits, 8–13 mm long. Fruits terete, narrowly linear, somewhat falcate, divaricate to ascending, 5–6.8 cm long, 1.4–1.6 mm wide; valves glabrous, smooth, conspicuously 3-veined; septum complete, prominently 3-veined; style slender, 1–2 mm long; stigma subentire. Seeds oblong, coarsely reticulate, uniseriately arranged, 1.4–1.6 mm long, 0.9–1 mm wide.

Sisymbrium morrisonii is named after John L. Morrison, a student of the Brassicaceae and one of the collectors of the holotype. It is closely related to the Peruvian endemic *S. gracile* Wedd. (= *S. macrorrhizum* (Muschler) J. F. Macbr.), from which it differs in having undivided leaves, larger flowers, slender styles, and longer fruits. *Sisymbrium gracile* has pinnatifid to pinnatisect middle leaves, smaller flowers, obsolete to stout styles less than 1 mm long, and fruits 3–4(4.5) mm long. Schulz (1924, 1936) segregated the latter (as *S. macrorrhizum*) to *Phlebiophragmus* O. E. Schulz, which he distinguished from *Sisymbrium* solely on the basis of having 2- to 4-veined instead of 1-veined or veinless septa. However, this feature is unreliable and does not justify recognition of *Phlebiophragmus* as an independent genus.

Sisymbrium morrisonii is also related to the Peruvian *S. oleraceum* O. E. Schulz. The latter has shorter fruits 4–4.5 mm long, glabrous stems and leaves, yellow petals to 6.5 mm long, and stout styles less than 1 mm long.

I am most grateful to Michael Dillon for sending the material of *Sisymbrium llatasii* for study, to the curators and directors of F, NY, and UC (abbreviations follow Holmgren et al., 1981) for sending the loans, and to Barbara Nimblett for typing the manuscript.

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—Ihsan A. Al-Shehbaz, *Arnold Arboretum, Harvard University, 22 Divinity Avenue, Cambridge, Massachusetts 02138, U.S.A.*

NOTICES

The 1989 Jesse M. Greenman Award

The 1989 Jesse M. Greenman Award has been won by Carol A. Todzia for her publication "Chloranthaceae: *Hedyosmum*," which appeared in *Flora Neotropica Monographs*, Volume 48. This monograph is derived from a Ph.D. dissertation submitted to the University of Texas, under the direction of Dr. Beryl B. Simpson. The genus *Hedyosmum* is comprised of 40 species of predominantly montane, neotropical shrubs and trees. The comprehensive monograph, which includes four newly described species, reexamines previous treatments of the genus and presents new data on anatomy, morphology, ecology, and geography. Synopses of the taxonomic history, palynology, cytology, and uses are also provided.

This award is named for Jesse More Greenman (1867–1951), who was Curator of the Missouri Botanical Garden Herbarium from 1919 until 1943. A cash prize of $500 is presented each year by the Garden, recognizing the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation published during the previous year. Nominations for papers published during 1989 are now being accepted for the 22nd annual award, which will be presented in the summer of 1990. Reprints of such papers should be sent to the Research Division, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. In order to be considered for the 1990 award, reprints must be received by 1 June 1990.

Volume 76, Number 4, pp. 945–1192 of the Annals of the Missouri Botanical Garden was published on November 7, 1989.

BOOK REVIEW

Godfrey, Robert K. 1988. Trees, Shrubs, and Woody Vines of Northern Florida and Adjacent Georgia and Alabama. ix + 734 pp., illus., Univ. of Georgia Press, Athens, Georgia, & London. ISBN 0-8203-1035-2. Price: $50 (cloth).

I have known, respected, and liked the writer for many years now and must state that it came as no surprise that the work is so good. It is equal to if not better than Godfrey's previous floristic works, *Trees of Northern Florida* (with H. Kurz) and *Aquatic and Wetland Plants of Southeastern United States* (with Jean W. Wooten).

Several factors make this new work as good as it is:

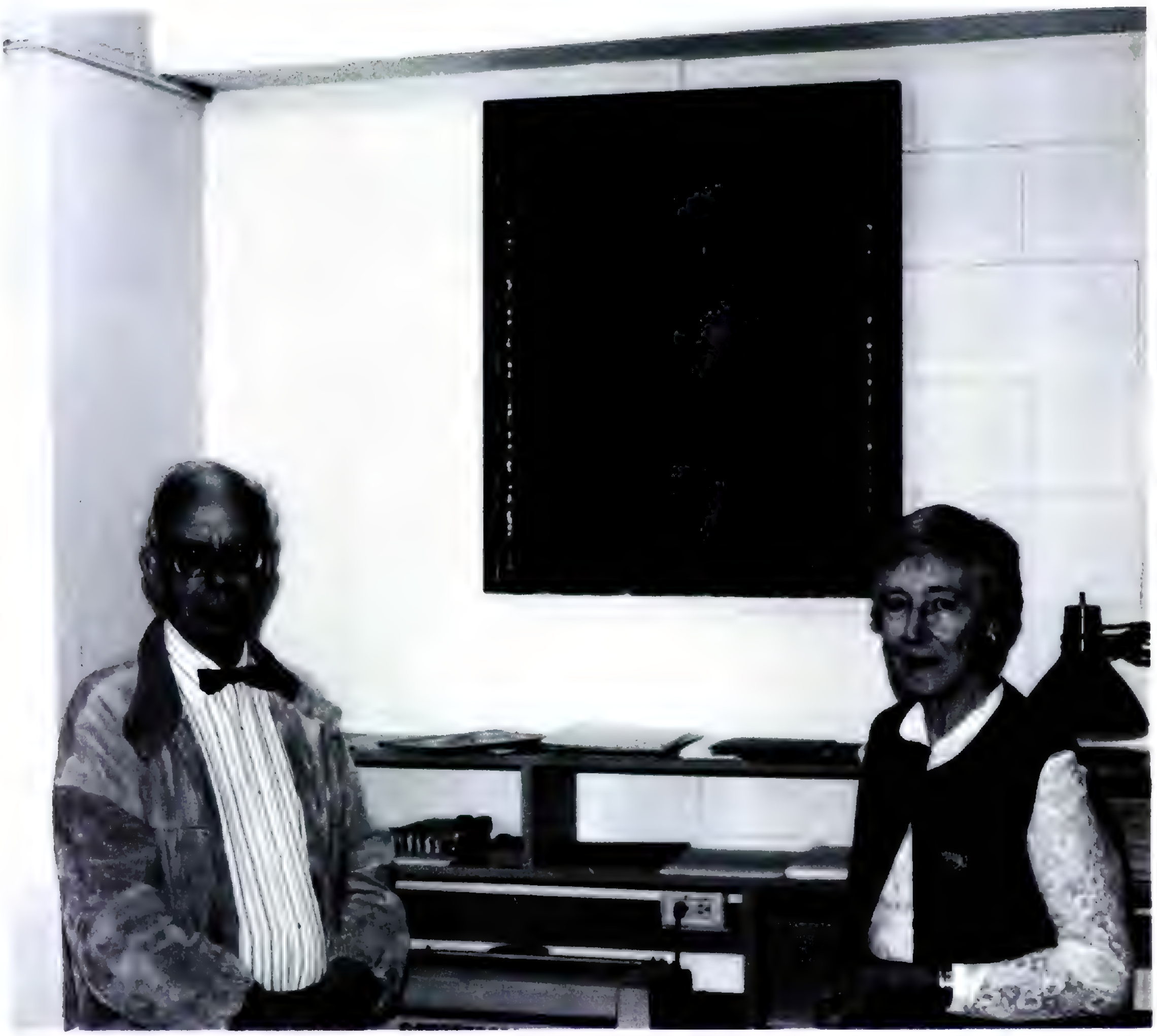
Robert Godfrey is one of the most perceptive people in botany, an indefatigable field man with a stack of full field notebooks reaching back to the 1930s. Few have exceeded him as a collector; fewer still have matched this taxonomist in interpretation of such field experience, and no other writer possesses quite the same style. Each clearly written description is a seemingly effortless rendition of observations accumulated the hard way over decades. Where there is a doubt or a difference or a wonder about something, that comes across.

The work is very well edited, primarily because there has been such consideration of the thorough and factually entertaining style unique to this man.

The illustrations are superb. They are botanical art in the best sense. The artist for most of them (Melanie Darst) has pleased the eye without sacrificing morphological detail. The teaching value of such work deserves highest praise.

The keys work.

Prediction of the popularity of such a book is a safe bet. This reference, handsomely and durably bound, will be mandatory equipment for and good company on any field trip for woody plants within the Southeastern U.S.A.—Robert Kral, *Director and Curator of the Herbarium, Box 1705, Station B, Vanderbilt University, Nashville, Tennessee 37235, U.S.A.*



Rolla Milton Tryon, Jr., and Alice Faber Tryon at Harvard University, October 1989. The portrait is of Daniel Cady Eaton (1834 1895), student of Asa Gray and first American pteridologist.

A Festschrift in Honor of Alice Faber Tryon and Rolla Milton Tryon, Jr.

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Annals of the Missouri Botanical Garden

A FESTSCHRIFT IN HONOR OF ALICE FABER TRYON AND ROLLA MILTON TRYON, JR.

David S. Barrington, Organizer[1]

> With the exception of *Dryopteris* and *Elaphoglossum* and a few small genera, not a single genus of American Ferns has been worked out monographically. The chaos and confusion in this group are really indescribable, the synonymy exceedingly complicated and intricate, the variation of many species amazing. . . . Domin (1929).

Karel Domin's lament, now 60 years old, provides the context for an appreciation of the immense contribution of Alice and Rolla Tryon to twentieth-century pteridophyte systematics. Armed with an exhaustive knowledge and innate appreciation of the organisms, supreme patience, and a remarkable talent for dismantling nomenclatural tangles, these two botanists have provided monographic treatments for an impressive number of taxa in the New World (e.g., A. Tryon, 1957, 1962, 1970; R. Tryon, 1941, 1942, 1955, 1960, 1970a, 1971a, 1976). These and related works have been included in a monographic synopsis of the entire diversity of New World ferns, with notes on their relationships to the remainder of the world's fern flora, in the monumental *Ferns and Allied Plants* (Tryon & Tryon, 1982). Domin's indescribable chaos has been substantially reduced to order.

The Tryons' contributions have not been limited to the field of systematics. Each has aggressively pursued basic problems in the evolutionary biology of pteridophytes that arose during the monographic work. Alice Tryon has specialized in fern spore architecture and evolution (e.g., A. Tryon, 1964, 1971, 1972, 1985, 1987), while Rolla Tryon has focused on biogeography and its role in the evolution of ferns (e.g., R. Tryon, 1944, 1956, 1970b, 1971b, 1972, 1986; R. Tryon & Gastony, 1975).

Inaugurated by the Tryons in 1970, the New England Fern Conference has been for 20 years a productive intellectual setting for students of fern biology to discuss the issues. A remarkable array of pteridophyte research projects has been conceived and developed in the seminar room at the Harvard Forest during the New England Fern Conferences. In addition to many of the research programs represented in this Festschrift, the work on genetic load and homoeologous pairing (Klekowski, 1973a, b), biochemistry of fern spore germination (DeMaggio & Raghavan, 1972; DeMaggio et al., 1980), autogamous allohomoploidy (Conant & Cooper-Driver, 1980), and secondary compounds in pteridophyte systematics, ecology, and evolution (e.g., Britton & Widén, 1974; Cooper-Driver, 1980; Cooper-Driver & Haufler, 1983; Richardson, 1984) were all discussed early in their development at New England Fern Conferences.

[1] Pringle Herbarium, Department of Botany, Burlington, Vermont 05405-0086, U.S.A.

Throughout these conferences, Alice and Rolla Tryon's interest in all aspects of fern biology has provided a stimulus and a focal point for a diversity of research efforts.

The Tryons have influenced the professional development of students in another way. Their field trips have introduced numerous professional botanists to the ferns of the American tropics. These trips, which exposed students to the nature of fern research in the tropics, have enriched the literature, in many cases as the students' first experiences of research and publication (e.g., R. Tryon et al., 1973; A. Tryon et al., 1975; R. Tryon & Conant, 1975; R. Tryon & Vitale, 1977).

Though their work continues apace, as the fascicles of the *Flora of Peru* appear (R. Tryon & Stolze, 1989a, b) and the authoritative monograph on fern spores of the world is readied for press (A. Tryon, 1990), we, pteridophyte biologists profoundly influenced by our contact with the Tryons, take this opportunity to honor Alice Faber Tryon and Rolla Milton Tryon, Jr., with a Festschrift on the occasion of their retirement from Harvard University. Our contributions are as diverse as the realm in which the Tryons have been influential in pteridology: history of systematics (Paris & Barrington), taxonomy and phylogeny (Hickey; Moran; Smith; Stolze), ecology (Cooper-Driver; Riba & Reyes J.), reproductive biology (Conant), evolutionary systematics (Barrington; Gastony; Haufler, Windham & Ranker), biogeography (Kramer), and molecular biology of hybridization (Stein & Barrington). Dr. Walter H. Hodge, who has contributed many high-quality photographs to Tryon publications, provided the portrait at the end of this Festschrift. We thank the Tryons for their contribution to our professional development and wish them all the best in their present endeavors.

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WILLIAM JACKSON HOOKER AND THE GENERIC CLASSIFICATION OF FERNS[1]

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ABSTRACT

Twentieth-century pteridologists (e.g., Copeland, Pichi Sermolli) have criticized the work of William Jackson Hooker, Director of Kew Gardens (1841–1865) and author of *Species Filicum*, claiming that his fern classification was regressive and that he impeded 19th-century progress in pteridology. In particular, Hooker's critics have objected to his large genera based almost exclusively on characters of the sorus. To test the contention that Hooker's system was regressive, we compared it with those of his contemporaries Presl, Fée, and Smith. We found that, although Hooker preferred to use reproductive characters to circumscribe genera, he made good use of vegetative features to delimit natural groups within them. His large genera are comparable to the tribes of other authors of his day, and his subgenera and sections are similar to their genera. Hooker's system is at least as modern as those of Presl and Fée, based on a comparison of the authors' treatments of the polypodioids. Smith produced the most insightful treatment of the group, but his work was largely ignored in his time. Of the four authors we discuss here, Hooker alone had a substantial impact on 19th-century pteridology; only his system was widely adopted, and it was not effectively challenged until the turn of the century. We note that many of the issues that surrounded generic classification in Hooker's time, e.g., what size of genus to accept, are still unresolved today.

> In the time of Smith and Fée and such contemporaries as Kunze, immediately preceding the *Origin of Species*, pteridology was perhaps the most advanced division of botany. Affinity was a word in common use, and, except that it lacked a philosophical foundation, it seems to have meant very much what it means today. Under the incubus of Hooker's prestige, earned by his monumental work on species and effective in spite of his archaic attitude on genera, pteridology lost its advanced position, and in forty years became one of the most backward divisions.

With these words Copeland (1947) summarized the response of many 20th-century pteridologists to the life and work of William Jackson Hooker, 19th-century author of the monumental *Species Filicum* (1844–1864) and numerous other works on fern classification. Although Copeland's comments stand out in the severity of the criticism, they are by no means atypical. Pichi Sermolli (1973), for example, wrote:

> If Presl did not receive the attention he deserved, this was due to the influence exercised at that time by W. J. Hooker, whose preference for large genera, based solely on the characters of the sori and the sporangia, is well known to all pteridologists.

In general, Hooker's classification has been called regressive with respect to those of his contemporaries. To determine whether this is accurate, we compared Hooker's classification with those of Presl, Fée, and Smith, all of whom history has treated more favorably. The systems were compared with reference to hierarchical organization, characters used at various hierarchical levels, and the extent to which each author succeeded at producing a natural classification of a problematic group, the polypodioid ferns. We present evidence that Hooker's modern critics have judged his work unfairly: Hooker's classification was as insightful as those of his more highly regarded contemporaries, but he has been criticized because he adopted a broad genus concept.

Hooker's system has also been described as an impediment to progress in pteridology. We explored this idea by evaluating the impact of the various mid-19th-century fern classifications. To

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do this we determined (1) how widely the various authors were followed in floristic treatments of the day, and (2) the effect of Hooker's published work on the volume of subsequent pteridological research in the 19th century. Here we concur with the critics: Hooker's scheme was followed more widely than any other mid-19th-century classification, and the volume of systematic work produced in pteridology was reduced following *Species Filicum*.

To put the problem in context, we first present a brief account of Hooker's life and the intellectual climate in which he worked.

A Synoptical Account of the Life and Work of William Jackson Hooker

William Jackson Hooker (1785–1865), born into a well-to-do Norwich family and raised in the tradition of the gentleman naturalist, made his first contributions to botany in the field of bryology. His early work on mosses brought him to the attention of Joseph Banks, Robert Brown, and other prominent naturalists of his day, and prompted Hooker's election to the Linnaean Society in 1806. For additional information on Hooker's early life, the reader is encouraged to consult Allan's (1967) excellent biography.

Hooker first turned his attention to the ferns during his tenure as Regius Professor of Botany at Glasgow University. His first major contribution to pteridology was *Genera Filicum* (1838–1842), a set of engravings by Bauer with accompanying text by Hooker. The circumscription and definition of the fern genera in that work follows the system proposed by the Czech pteridologist Presl in his *Tentamen Pteridographiae* (1836).

In 1841, Hooker was appointed Director of the Royal Gardens at Kew. During his 25 years as director, Kew was built up from the Queen's kitchen garden to one of the world centers of botanical research, boasting an incomparable library and herbarium, acres of glasshouses and outdoor gardens, an arboretum, and a museum of economically important plants. As Director of Kew, Hooker also did much to promote the study of botany in Great Britain. For instance, through his contacts around the world, often his former students at Glasgow or connections in business and government, Hooker amassed an enormous private herbarium, which he made freely available to the botanical community.

Hooker secured his role as eminent pteridologist with the publication of *Species Filicum*, the magnum opus of his pteridological career. Published in five volumes between 1844 and 1864, the work included detailed descriptions of all known ferns, including distributional information, collection numbers, and illustrations. In *Species Filicum* Hooker abandoned the precedent set by Presl (1836) and produced his own classification of the ferns. Wishing to present a condensed version of the work that could be used in the field, Hooker began *Synopsis Filicum* in 1865. In August of that year, after just 22 pages of the manuscript had been submitted, Hooker died of diphtheria, then epidemic at Kew. *Synopsis Filicum* was completed by Baker, an assistant curator at the Royal Gardens, who finished the manuscript using Hooker's notes, herbarium collections, and an annotated copy of *Species Filicum*. The *Synopsis* was finished in 1868; a second edition containing an appendix with many species newly described by Baker was published in 1874.

Hooker's Milieu: Fern Classification in the Mid-19th Century

The years in which Hooker produced his major works on fern classification, 1844 to 1865, follow the death of Linnaeus (1778) and mostly precede the 1859 publication of Darwin's *Origin of Species*. In this period, the Natural Method of classification developed by M. Adanson, B. de Jussieu, and A.-L. de Jussieu had become well established in flowering plant taxonomy and had largely displaced the Linnaean Sexual System. Under the Natural System, characters from all parts of the plant body came to be used to define plant groups and to assess relationships among them. In contrast to Linnaeus's system, which emphasized characters of the reproductive body (the "fructification"), no characters were to receive a priori weighting; all were considered potentially informative. The value of any particular character was determined only following an evaluation of the constancy of that character and its correlation with other characters in the group of interest (Tryon, 1952).

A natural taxon, then as now, was one that had a real existence in nature. However, in the years before Darwin, relationships among species and higher taxa were interpreted, not in the genealogical sense, but as variations on a pure form that existed in the mind of the Creator. The goal of Natural Classification was a system that revealed the Creator's mind as evidenced in His creation.

In the first half of the 19th century, changes in the approach to fern classification were taking place that paralleled those in the classification of flowering plants. At the start of the century pteridology was still under the influence of the Linnaean system. The major classifications produced around

that time, Sir J. E. Smith's "Tentamen botanicum de Filicum generibus dorsiferarum" (1793) and Olaf Swartz's 1806 handbook *Synopsis Filicum*, were based almost exclusively on the shape and position of the sorus and the indusium. Using those characters, Smith and Swartz arranged the several hundred known fern species into 20 and 38 genera, respectively.

By 1836, however, a new approach to the classification of ferns was evident. That year marked the beginning of 40 years of great activity in pteridology, a period in which the old Linnaean methods were set aside and the Natural System was adopted in fern classification. Four men figure prominently in this period: Karl Boriwog Presl, Antoine Laurent Apollinare Fée, John Smith, and William Jackson Hooker.

In 1836, K. B. Presl of Prague published the *Tentamen Pteridographiae*. His system relied on attributes of the rhizome, petiole vasculature, indument, venation, and size and form of the parenchyma cells, as well as those of the sorus. The use of many characters, both reproductive and vegetative, permitted Presl to resolve 112 fern genera among the polypodioid (sensu lato), cyatheoid, and gleichenioid ferns. Subsequently, Presl (1843, 1845, 1847, 1852) expanded his classification to include the rest of the homosporous ferns, bringing the total number of his genera to 176 (Tryon, 1952).

A second classification of ferns published during the middle years of the 19th century was the *Genera Filicum* (1850–1852) of A. L. A. Fée, a French pteridologist working at Strasbourg. In that work, Fée treated 181 genera of polypodioid and cyatheoid ferns. The characters he used were primarily those used by Presl (1836), but Fée also noted the number of cells in the annulus and spore shape. These new characters were more useful in the delimitation of genera than of higher groups, so the resultant classification, while more elaborate than Presl's, did not substantially improve upon it (Pichi Sermolli, 1973).

John Smith, a gardener at Kew between 1822 and 1864, was another important contributor to pteridology in this period. His knowledge of ferns, based on daily observations of living plants in cultivation at Kew, led Smith to publish his ideas on their relationships in a treatise entitled "An arrangement and definition of the genera of ferns" (1841–1843). In that work, he used combinations of vegetative and reproductive characters to define 143 genera of filicalean ferns. Although Smith developed his system without having seen Presl's 1836 *Tentamen*, the overall structure of the two classifications and the number of genera recognized in each were remarkably similar. In 1875, Smith published his second major classification, *Historia Filicum*, reflecting the experience of more than 30 years since "An arrangement and definition of the genera of ferns" was published. Using a combination of vegetative characters, including vernation of the croziers, rhizome habit, petiole articulation, and leaf venation, together with the reproductive characters mentioned previously, Smith defined 220 genera of ferns, many constituted as they are today.

The fourth major figure in mid-19th-century pteridology was William Jackson Hooker. Hooker completed most of the the work on his *Genera Filicum* during his years at Glasgow. There is no evidence that he had great experience with the ferns at that time, so perhaps it is not surprising that he adopted Presl's circumscription and arrangement of fern genera. Of the 135 genera included in *Genera Filicum*, the circumscription of 115 followed Presl (1836); the 20 not included in the *Tentamen* were adopted from Smith (1841–1843). Hooker's admiration of Presl's work is evident in the preface of the *Genera Filicum*, in which he praises the *Tentamen* for the accuracy of the research and for the "clear and perspicuous" arrangement of the genera presented therein. That he nevertheless had some reservation about Presl's genera and the characters used to circumscribe them is evident when he wrote that perhaps too much emphasis is placed on the number and position of vascular bundles in the petiole, and that venation "holds too prominent a place in the generic character" (Hooker, 1838–1842). Hooker reserved for himself the right to reconsider his endorsement of Presl's genera as he prepared *Species Filicum* (Hooker, 1838–1842). That Hooker did change his mind substantially is evident in the classification he presented in those volumes. In *Species Filicum*, he circumscribed genera almost exclusively on the basis of soral characters. As a result, the 135 genera of the *Genera Filicum* were reduced to 63.

The substantial change in Hooker's approach to generic classification between the completion of *Genera Filicum* and the initiation of *Species Filicum* is attributable to his change of mind about the kinds of characters useful in circumscribing genera. As a Glasgow professor, Hooker had endorsed Presl's use of vegetative characters; as chief botanist at Kew, he relied almost entirely on characters of the fructification. Although Hooker never published an explicit justification of his revised approach to fern classification, it appears that con-

venience was a major factor in his decision (Tryon, 1952). As curator of ferns at Kew Gardens, then the largest botanical research center in the world, Hooker had the task of processing the enormous volume of collections arriving at the herbarium from around the world. Given that task, it is no wonder he preferred to use characters that could readily be evaluated from herbarium specimens. Characters of the sorus, especially shape and position, are easy to evaluate on herbarium specimens, whereas those of the petiole vasculature often are not. That it was specifically convenience Hooker was seeking in his choice of reproductive characters, and not some Linnaean concept of the essential nature of those characters, is evident in his comment that Presl had "laid too much stress on the number and other circumstances connected with the bundle of vessels in the stipe, which in the Herbarium are difficult of investigation" (Hooker, 1838–1842).

Hooker was also concerned that his works on fern taxonomy be useful to the amateur. Having argued against the usefulness of annulus position as a generic character, he went on to say that it would be inconvenient to maintain even a group or a section on the basis of that character in "a work whose main object is to assist the tyro in the verification of genera and species" (Hooker, 1838–1842).

Was Hooker's Classification of the Ferns Regressive?

To determine whether Hooker's 20th-century critics have been justified in calling his work regressive with respect to that of his contemporaries, we compared the systems presented in the *Tentamen Pteridographiae* (Presl, 1836), *Genera Filicum* (Fée, 1850–1852), *Synopsis Filicum* (Hooker & Baker, 1874), and *Historia Filicum* (Smith, 1875). Particular attention was given to the hierarchical structure of each author's classification and to the characters used at various levels in the hierarchy. To determine how well each author's chosen characters resolved natural relationships, we made a detailed comparison of the authors' treatments of the polypodioids. This group was chosen first because its circumscription and definition has a history of confusion, and second, because there is now a reasonable consensus on how the polypodioids should be treated.

HIERARCHICAL STRUCTURE

To compare the hierarchical structure of the four classifications, we first reviewed each of the four principal works to determine which taxonomic categories were used and how they nested. To make the comparison, we ranked the supraspecific categories by number, with I being the fundamental division of the Filicopsida and so forth (Fig. 1). We found that the authors differed substantially in their use of categories. This is perhaps not surprising, since the use of taxonomic categories had not yet been stabilized by the International Code of Botanical Nomenclature (Lawrence, 1951). For example, the rank "section" was used above the genus level by Presl, below it by Hooker, and both above and below the genus level by Smith. We then compared the position of the genus in the hierarchy, and the use of subordinate categories to resolve infrageneric relationships (Fig. 1). Notice that, whereas both Presl's and Fée's genera are at approximately the same level in the hierarchy, reflecting their similar concepts of the genus, Hooker's genus occupies a higher level. He makes frequent use of infrageneric categories (often unnamed) to designate natural groups within the genus, as many as four in the case of large genera such as *Polypodium*. Smith, by contrast, used the genus at a much lower level in his hierarchy and never used more than one infrageneric category above species.

CHARACTERS USED AT EACH LEVEL IN THE HIERARCHY

To determine what kinds of characters the authors used to circumscribe taxa at each rank, we ordered the characters according to the frequency with which each was employed at a given rank, omitting those characters that were seldom used (Fig. 1). We found that, with one exception, all four authors used characters of the reproductive body at the highest levels of their classifications. Smith was exceptional in his use of two vegetative characters, internode length and articulation of petiole to rhizome, to establish his fundamental division of the ferns. Although these characters proved to be powerful in elucidating relationships among genera and tribes, Smith's use of them at the highest level overemphasized their importance. His decision led to an improbable alliance of all species with leaf bases articulate to the rhizome, a distinct flaw in a system that was otherwise fairly insightful.

In their circumscription of genera, Presl, Fée, and Smith all used vegetative features such as venation, leaf architecture, and rhizome structure (Fig. 1). Hooker, however, made infrequent use of such characters. All of his genera were circum-

	PRESL	FÉE	HOOKER	SMITH
I	ANNULUS POSITION subordo	ANNULUS POSITION -atae	ANNULUS POSITION VERNATION SPORANGIUM DEHISCENCE suborder	PETIOLE ARTICULATION INTERNODE LENGTH division
II	INDUSIUM PRESENCE /ABSENCE cohors	SORUS SHAPE -taxiocarpeae	INDUSIUM PRESENCE /ABSENCE -ae	ANNULUS POSITION (unnamed) A
III	INDUSIUM STRUCTURE SORUS SHAPE, POSITION tribus	SORUS SHAPE, POSITION INDUSIUM PRESENCE /ABSENCE -eae	SORUS SHAPE, POSITION INDUSIUM STRUCTURE SPORANGIUM STALK PRESENCE/ABSENCE ANNULUS POSITION, FORM tribe	INDUSIUM PRESENCE /ABSENCE (unnamed) *
IV	SORUS SHAPE, POSITION INDUSIUM STRUCTURE sectio	INDUSIUM STRUCTURE SORUS POSITION INDUSIUM PRESENCE /ABSENCE -eae	**SORUS SHAPE, POSITION** **SPORANGIUM NUMBER** **LEAF ARCHITECTURE** **INDUSIUM POSITION** **VENATION** **HABIT** **genus**	SORUS SHAPE, POSITION INDUSIUM STRUCTURE, PRESENCE/ABSENCE VENATION LEAF ARCHITECTURE HABIT tribe
V	**VENATION** **INDUSIUM STRUCTURE** **SORUS POSITION** **genus**	**VENATION** **LEAF ARCHITECTURE** **INDUMENT** **INDUSIUM STRUCTURE** **genus**	PETIOLE ARTICULATION SORUS POSITION series	VENATION series
VI	LEAF ARCHITECTURE VENATION SORUS POSITION section	SORUS SHAPE, POSITION (unnamed) I	VENATION INDUSIUM STRUCTURE LEAF ARCHITECTURE section	VENATION SORUS SHAPE, POSITION LEAF ARCHITECTURE INTERNODE LENGTH INDUSIUM STRUCTURE section
VII	VENATION INDUMENT LEAF ARCHITECTURE (unnamed)	- (not used)	LEAF ARCHITECTURE (unnamed) *	**HABIT** **INTERNODE LENGTH** **SORUS SHAPE, POSITION** **LEAF ARCHITECTURE** **VENATION** **RECEPTACLE FORM** **genus**
VIII	VENATION (unnamed)	- (not used)	LEAF ARCHITECTURE (unnamed) +	HABIT INTERNODE LENGTH LEAF ARCHITECTURE section

FIGURE 1. Comparison of the hierarchical organizations of the classifications produced by our 19th-century authors. Characters are ranked according to the frequency with which they were used at each level in the hierarchy. The genus is highlighted in bold. The classifications being compared are as follows: Presl = Presl (1836); Fée = Fée (1850–1852); Hooker = Hooker & Baker (1874); Smith = Smith (1875).

scribed mostly with reproductive features, presumably because of the ease with which these could be evaluated. In his use of generic characters, Smith is again exceptional. Basing his genera on a combination of reproductive and vegetative features and weighting them equally, Smith more nearly approximated the ideals of the Natural System than did his contemporaries.

RESOLUTION OF NATURAL GROUPS: THE POLYPODIEAE

To evaluate the success of our authors in resolving natural groups, we compared their treatments of the polypodioid ferns. In each treatment that alliance was defined as the group of ferns with round, exindusiate sori; by choosing such a broadly defined assemblage, we had the opportunity to determine how well each author used vegetative characters to order variation within the alliance. In particular, we attempted to determine how well the 19th-century pteridologists drew the distinction between the polypodioid ferns and the phegopteroids, a group aligned with the thelypteroids in modern classifications (Copeland, 1947; Tryon & Tryon, 1982). The two share the character of round, exindusiate sori, but the phegopteroids differ in a suite of other important attributes, such as petiole articulation, leaf indument, and spore morphology.

Nineteenth-century treatments of the polypodioids were compared with reference to two criteria: (1) Did the author in question avoid the inclusion of extraneous elements within his Polypodieae? In particular, did he draw the distinction between the polypodioids and the phegopteroids? and (2) Did he assemble the polypodioids—as we currently understand them—together in one place, or were they scattered among other tribes? Our analysis was made with reference to Copeland (1947) and Tryon & Tryon (1982), two well-known and widely followed 20th-century treatments.

Within Presl's sect. Polypodieae, elements of diverse affinities are intermixed, sometimes without apparent pattern (Table 1). *Phegopteris*, for example, is included in Presl's genus *Polypodium*. This is surprising, since he was alert to the problem of distinguishing the exindusiate aspidioids (i.e., the phegopteroids) from the polypodioids (Presl, 1836, p. 167). Using round, exindusiate sori with punctiform receptacles located on veins, Presl assembled in the tribe Polypodieae approximately half of the elements placed there by modern authors. Other polypodioids were included in his Acrosticheae (those with sporangia distributed over the abaxial surface of the leaf—a character that has arisen in several different lineages), Grammitideae (those with more or less elongate receptacles), and Taenitidae (those with sporangia borne on long, inframarginal commissures).

Fée followed Presl quite closely, as is evident in their treatments of the polypodioids (Table 1). Like Presl, Fée included dipterids, dryopteroids, gymnogrammoids, and thelypteroids within his Polypodieae. Fée recognized *Phegopteris* as a separate genus, following *Polypodium*. Also like Presl, Fée included about 50% of the modern polypodioids in his Polypodieae. Because he accorded great importance to the position of the sporangia relative to the fertile veins, the remaining polypodioids are scattered throughout tribes of diverse affinity in Fée's system.

The monotypic Polypodieae of Hooker comprised *Polypodium*, which included more than 400 species. Within *Polypodium*, however, Hooker made extensive use of infrageneric categories, enabling him to circumscribe some reasonably natural groups. For instance, by drawing an early distinction between the Eremobryoid series, with articulate petiole bases, and the Desmobryoid series, without them, he appropriately separated *Phegopteris* (as a section) from *Polypodium*. He placed true polypodioids in the Eremobryoid series, in sect. *Eupolypodium*. Although several grammitidoid species are also included here, they are a cohesive group of species placed at the beginning of the section, indicating that Hooker recognized their distinctiveness. His emphasis on sorus shape led Hooker to place a number of polypodioid genera in the Grammitideae (the next tribe in his sequence, with sori at least twice as long as broad) or the Acrosticheae. Nevertheless, he correctly classified almost two-thirds of modern polypodioid genera. Hooker did not always circumscribe groups so successfully, however. For example, his Grammitideae comprised a diverse assemblage of thelypteroids, cheilanthoids, vittarioids, and misplaced polypodioids.

By far the most modern treatment of the Polypodieae was that of John Smith. Although he mistakenly included two grammitidoid genera, his tribe was a remarkably natural assemblage, comprising more than 80% of the modern polypodioids. Smith's use of petiole-base articulation at the highest level in his classification was in this case an advantage: it separated *Phegopteris* from the polypodioids right from the start.

We conclude that Hooker's perception of natural relationships was at least as advanced as Presl's and Fée's. This is evident in a comparison of the three treatments of the phegopteroids relative to the polypodioids. All three erroneously included the phegopteroids in their Polypodieae. Hooker, however, indicated the distinctiveness of the phegopteroids by placing them, together with several other exindusiate thelypteroids and dryopteroids (taxa that have until recently been placed together in the Aspidieae), at the beginning of the Polypodieae. Furthermore, by placing them immediately following the Aspidieae, Hooker apparently implied an

TABLE 1. Mid-19th-century systematic treatments of the polypodioids, with reference to recent systematic opinion. Letters in parentheses represent taxon's placement in Copeland (1947) and/or Tryon & Tryon (1982). (P) = Polypodieae (sensu Tryon & Tryon, 1982); (G) = Grammitidaceae; (T) = Thelypteridaceae; (A) = Dryopteridaceae; (D) = Dipteridaceae. Numbers and other symbols (e.g., +, **) are those used by the authors in the original publications.

Presl, 1836	Fée, 1850–1852	Hooker & Baker, 1874	Smith, 1875	Smith, 1875 (continued)
Subordo II. Cathetogyratae	Polypodiacees	Suborder II. Polypodiaceae	DIVISION I. EREMOBRYA	Sect. 6—Pleopelteae
Cohors II. Gymnosoreae	Cathetogyratae	B. Exinvolucratae	A. (Annulus vertical)	(P) 26. Lopholepis
Tribus VIII. Polypodiaceae	Taxiocarpeae	Tribe XI. Polypodieae	Tribe 3. Polypodieae	(P) 27. Lepicystis
Sectio II. Polypodieae	A. Gymnosoria	48. Polypodium	Sect. 1—Polypodeae	(P) 28. Pleopeltis
75. Polypodium	2. Polypodieae	*Desmobryoid series	(G) 5. Prosaptia	(P) 29. Paragramma
(G, P) Section Ctenopteris	(P) 108. Plecopteris	(T) Sect. Euphegopteris	(G) 6. Cryptosorus	(P) 30. Dictymia
(T) Section Phegopteris	(G) 109. Cryptosorus	(A) Sect. Cyrtomiphlebium	(P) 7. Thylacopteris	(P) 31. Anapeltis
(T) 76. Goniopteris	(G) 110. Grammitis	(T) Sect. Goniopteris	(P) 8. Polypodium	(P) 32. Microgramma
(A) 77. Pleocnemia	(P) 111. Polypodium	(A) Sect. Dictyopteris	Sect. 2—Goniophlebiae	...
(A) 78. Amblia	(T) 112. Phegopteris	**Eremobryoid series	(P) 9. Goniophlebium	...
(P) 79. Goniophlebium	(T) 113. Goniopteris	(P) Sect. Eupolypodium	(P) 10. Schellolepis	...
80. Marginaria	(P) 114. Goniophlebium	(P) Sect. Goniophlebium	(P) 11. Phlebodium	DIVISION II. DESMOBRYA
(P) Section Pleurogonium	(P) 115. Campyloneuron	(P) Sect. Phlebodium	Sect. 3—Pleurideae	I. (Annulus vertical)
(P) Section Marginaria	(P) 116. Lecanopteris	(P) Sect. Campyloneuron	(P) 12. Pleuridium	Tribe 13. Phegopterideae
(P) 81. Campyloneurum	(P) 117. Niphobolus	(P) *(unnamed)	(P) 13. Campyloneurum	Sect. 7—Phegoptereae
(P) 82. Pleopeltis	(P) 118. Craspedaria	(P) **(unnamed, = Niphobolus)	(P) 14. Niphobolus	(T) 123. Phegopteris
(A) 83. Dictyopteris	(P) 119. Chrysopteris	Sect. Phymatodes	(P) 15. Niphidium	
84. Phymatodes	(P) 120. Aglaomorpha	(including Pleopeltis)	(P) 16. Colysis	
(P) Section Euphymatodes	(A) 121. Dictyopteris	*(unnamed)	(P) 17. Selliguea	
(P) Section Pleuridium	(P) 122. Microsorium	(P) + (unnamed)	Sect. 4—Phymatodeae	
(P) Section Drynaria	(P) 123. Drynaria	(P) ++ (unnamed, = Pleuridium)	(P) 18. Phymatodes	
(P) 85. Psygmium	(P) 124. Pleuridium	**(unnamed)	(P) 19. Phymatopsis	
86. Niphobolus	(D) 125. Dipteris	(P) + (unnamed)	(P) 20. Niphopsis	
(P) Section Niphobolus	(P) 126. Dryostachyon	(D) ++ (unnamed, = Dipteris)	(P) 21. Lecanopteris	
(P) Section Cyclophorus		***(unnamed)	Sect. 5—Drynariae	
(P) Section Scytopteris		(P) + (unnamed)	(P) 22. Drynaria	
Sectio III. Lecanopterideae		(P) ++ Drynaria	(P) 23. Dryostachyum	
(P) 87. Lecanopteris			(P) 24. Aglaomorpha	
(G) 88. Calymmodon			(P) 25. Artheromeris	

affinity of the phegopteroids to the aspidioids. (Although he asserts that the phegopteroids should certainly be maintained within *Polypodium*, Hooker notes that the aspidioid genus *Lastrea*, when its indusium has fallen off, is "impossible to distinguish" from the phegopteroids [Hooker, 1844–1864, vol. 4, p. 231]). Presl's and Fée's phegopteroids, by contrast, were interspersed among the true polypodioids. Although it is true that Hooker's choice and weighting of characters led him to form some assemblages that we recognize today as polyphyletic, e.g., his Grammitideae, his contemporaries made similar errors for similar reasons. It seems, then, that the criticism of Hooker's work has been elicited primarily by the breadth of the genera he recognized, not by his failure to perceive natural groups within them. At the generic level, Smith's system was by far the most modern. His faithful use of equally weighted characters from all parts of the plant body yielded genera that are quite natural by today's standards.

Note that, although the 19th-century pteridologists explained their taxa differently (i.e., as the products of creation, not evolution), they had the same goal as 20th-century systematic biologists: circumscribing groups with a real existence in nature. We therefore maintain that it is appropriate to evaluate the systems of the 19th-century pteridologists by comparing them to modern schemes. It is a tribute to all of the mid-19th-century pteridologists that major segments of their systems survive in modern classifications, though they had neither the data sets (e.g., chromosomal and biochemical) nor the analytical methods available now.

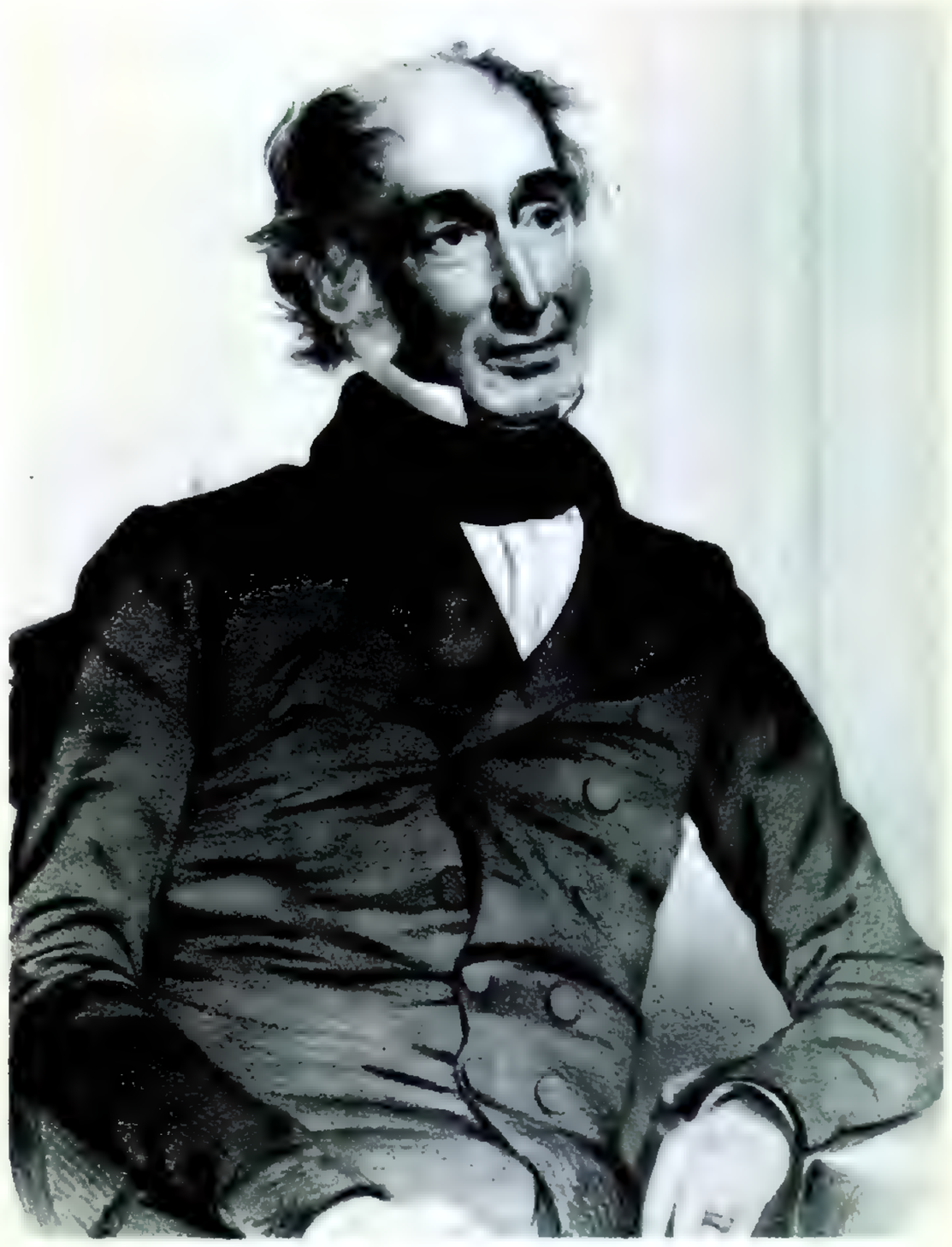

FIGURE 2. Sir William Jackson Hooker, 1851. (*Ipswich Museum Portraits* series by T. H. Maguire, artist and engraver. Courtesy of Hunt Institute for Botanical Documentation, Carnegie Mellon University, Pittsburgh, Pennsylvania.)

Did Hooker's System Impede the Progress of Fern Classification in the 19th Century?

To determine whether Hooker in fact impeded the development of fern classification in the 19th century, we first had to determine whether his system was adopted and, second, whether there was a reduction in the amount of work done on pteridophyte classification in the years after his publication of *Synopsis Filicum*.

To assess the impact of the various mid-19th-century classifications on the systematic community, we surveyed 22 floras published between 1876 and 1900 to determine which of the major classifications their authors followed in their treatments of the ferns (Table 2). We were able to do so because each system has a unique sequence of higher taxa; e.g., the polypodioids are placed near the end of the sequence in the systems of Hooker, Fée, and Presl, whereas Smith placed them near the beginning. Our review showed that there were two systems in common use during the period: Hooker's system and that of Endlicher, set forth in his *Genera Plantarum* (1836–1840). (Endlicher's system is almost identical to that used by Mettenius in his *Filices Horti Botanici Lipsiensis* [1856], but Endlicher's work predates Mettenius by almost 20 years. This suggests that the system presented in Mettenius and attributed to him by various authors [e.g., Bower, 1926, pp. 57–58; Pichi Sermolli, 1973] was not original. For this reason we have not included Mettenius in our comparison of the 19th-century pteridologists.)

We found that, of the 22 floras we surveyed, 11 followed Endlicher (North America and continental Europe), seven followed Hooker (British Empire and Latin America), and three used, to a greater or lesser extent, the older system of Swartz (1806). Smith's system was adopted in only one of the floras, and none followed Presl or Fée. Hooker's influence, then, if not global, was at least more widespread than that of his contemporaries, whose efforts seem to have been largely overlooked by

TABLE 2. Fern classifications followed in floristic works, 1876–1900. Endlicher = Endlicher, 1836–1840; Hooker = Hooker & Baker, 1874; Swartz = Swartz, 1806; Smith = Smith, 1875.

Author	Date	Geographic region	Taxonomic system
Eaton, D. C.	1877–1880	North America	Endlicher
Orcutt, C. R.	1885	California	Endlicher
Tracy, S. M.	1886	Missouri	Endlicher
Underwood, L. M.	1888	North America	Endlicher
Gray, A.	1889	northeast North America	Endlicher
Jesup, H. G.	1891	New Hampshire	Endlicher
Rand, E. L. & J. H. Redfield	1894	Maine	Endlicher
Deane, W.	1896	Massachusetts	Endlicher
Dodge, R.	1896	New England	Endlicher
Garcke, F. A.	1885	Germany	Endlicher
Koch, W. D.	1892–1907	Germany & Switzerland	Endlicher
Hooker, J. D.	1878	Great Britain	Hooker
Beddome, R. H.	1883	India	Hooker
Druce, G. C.	1886	England	Hooker
Jenman, G. S.	1890–1898	Jamaica	Hooker
Bailey, E.	1882	Hawaii	Hooker
Alfaro, A.	1887	Costa Rica	Hooker
Sodiro, A.	1890–1895	Ecuador	Hooker
Hillebrand, W. F.	1888	Hawaii	Swartz
Knuth, P. E.	1887	Schleswig-Holstein	similar to Swartz
Nöldeke, J. L.	1890	northern Germany	similar to Swartz
Potonié, H.	1889	Germany	similar to Smith

floristicians and others who might have put them to practical use.

Another indication of the extent of Hooker's influence on pteridology is the extent to which publication in the field was affected by his output. As we have seen, 1836–1865 was a period of great activity in fern systematics: major treatments were published every few years. Following the completion of Hooker's *Synopsis Filicum* (1868), however, Smith's *Historia Filicum* (1875) was the only major contribution published until almost the end of the century. Christ's 1897 publication of *Die Farnkrauter der Erde* struck the first blow at the hegemony of the Hookerian system, but it was in Diels's treatment of the ferns (1899–1900) in Engler and Prantl's *Natürlichen Pflanzenfamilien* that a new classification "far more in accordance with the modern view of phylogeny as the basic principle of systematics" was set forth (Christensen, 1938; see also Tryon, 1952). Thus it appears that Hooker's prolific output in the years 1846–1865 did indeed have a stifling effect on new work in pteridology.

WHY WAS HOOKER MORE INFLUENTIAL THAN HIS CONTEMPORARIES?

Given that Presl, Fée, Hooker, and Smith all contributed substantially to the mid-19th-century renaissance in pteridology, it is not at first clear why Hooker's work was the most influential. The triumph of Hooker's system may be attributable to several factors. First, as Hooker was Director of the Royal Gardens at Kew, his opinions carried the weight of authority. Also, he wrote in English at a time when British influence spanned the globe. Finally, because the classification presented in *Species Filicum* was summarized in the portable *Synopsis*, Hooker's views were readily accessible to collectors; the utility of the *Synopsis* was thus a major factor in the widespread acceptance of his system (Tryon, 1952).

By contrast, consider the positions of Hooker's contemporaries and the impact that they might be expected to produce on pteridology in their time. There was Presl, whose work was highly regarded among a small group of experts, but who worked in Prague and wrote in Latin at a time when scientific prose was being written more and more commonly in the vernacular. There was also Fée, whose writings were in French and Latin. Finally there was John Smith, gardener at Kew, who spent 20 years working in the service of its celebrated director. Although Smith's generic classification was easily the most modern among the systems we compared, Smith was overshadowed by the persona and reputation of Hooker, and his work was largely ignored. Only in this century has Smith been rec-

ognized as a pioneer of modern pteridology (Christensen, 1938; Tryon, 1952).

Conclusions

Having evaluated the contentions of Hooker's critics, we are in a position to ask whether they judged his works fairly. On the whole, we conclude that they did not: critical analysis of Hooker's work demonstrates that he had a reasonably advanced perception of natural relationships relative to most of his contemporaries. His system cannot fairly be called regressive just because of his broad genus concept. Today, more than 120 years since Hooker's death, generic concepts still vary widely among systematists, as at least two recent symposia on the subject attest ("Generic Concepts in the Compositae," American Institute of Biological Sciences [A.I.B.S.], 1983; "The Concept of the Genus," A.I.B.S., 1987; see also Stevens, 1985). Arguments about the criteria by which genera should be recognized and the kinds of characters useful in generic delimitation are as yet unresolved (Davis, 1987). Also unsettled is the question of whether (or under what circumstances) it is more useful to recognize large, often polymorphic genera that are well established in the taxonomic literature, or smaller, distinctive, segregate genera (Wagner, 1987; Young, 1987). Despite more than a century of systematic research since Hooker, there is no more of a consensus on generic classification than there was in his time. It is thus superficial to compare Hooker's system unfavorably with those of his contemporaries because he recognized fewer genera.

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STUDIES OF NEOTROPICAL *ISOËTES* L. I. *EUPHYLLUM*, A NEW SUBGENUS[1]

R. James Hickey[2]

ABSTRACT

A new subgenus in *Isoëtes*, *Euphyllum*, is proposed for three extant species and for members of the fossil genus *Isoëtites*. This new subgenus is distinguished from subg. *Isoëtes* by the possession of a number of plesiomorphic characters, including completely alate leaves and the absence of peripheral fibrous bundles. Descriptions and a key to the three modern species of *Euphyllum* are presented.

Our perception and understanding of the morphology and anatomy of *Isoëtes* is primarily a result of studies of north temperate species. Such a bias is a reflection of the availability of material and of the historical distribution of plant anatomists, morphologists, and taxonomists. Much of the diversity in this genus, however, occurs among the largely unstudied tropical representatives. Recently, Hickey (1986a) described a new *Isoëtes* with a completely alate (= laminate) leaf. In that paper, the genus was hypothesized as comprising two basal evolutionary groups: an alate grade association, consisting of three recent taxa plus the fossil genus *Isoëtites*, and a subulate (= nonalate) monophyletic lineage comprising the rest of the genus recognized here as subg. *Isoëtes*. The former group merits recognition as a separate subgenus based on its unique morphology and distinctively primitive leaf architecture and leaf base characters. This subgenus, *Euphyllum*, is described here and its three extant species are reviewed.

KEY TO THE SUBGENERA OF *ISOËTES*

1a. Leaves completely laminate, without a distal subula ..... subg. *Euphyllum*
1b. Leaves partially laminate, with reduced alae and a distal subula ..... subg. *Isoëtes*

Isoëtes subg. **Euphyllum** Hickey, subg. nov. TYPE: *Isoëtes gigantea* U. Weber, Nova Hedwigia 63: 245. 1922.

Subgenere *Isoëte* a quo foliis omino lamellatis differt.

Corms essentially globose, 2- or 3-lobed; dichotomous roots arising synchronously within the circumbasal fossa(e). Leaves numerous, spirally arranged, flattened to elliptic in cross section, completely alate; fibrous bundles absent; scales and phyllopodia absent. Sporangia ovate to obovate in face view, superficial or slightly embedded in leaf tissue, basal or elevated, the walls concolorous. Velum poorly developed. Ligule delicate, the margins ephemeral. Labium large, covering the ligule. Megaspores globose, trilete, variously patterned. Microspores ellipsoid, monolete, variously patterned.

Subgenus *Euphyllum* is a paraphyletic assemblage characterized and defined by the presence of completely alate leaves, a character considered to be plesiomorphic on the basis of its presence in the sister group Selaginellaceae and the outgroup Lycopodiaceae. Members of this subgenus frequently show a number of other plesiomorphic conditions, such as superficial sporangia (in *I. gigantea* and *I. bradei*), little or no velum coverage (all members), a lack of peripheral fibrous bundles (all members), and a distinctly narrowed leaf attachment (*I. gigantea* and *I. bradei*). In addition, megaspores of the extant members of the subgenus have surface morphologies roughly referable to the tuberculate morphology class, a condition also considered to be ancestral (Hickey, 1986b).

The alate character condition of the leaves in subg. *Euphyllum* contrasts sharply with the condition found in the rest of the genus. In subg. *Isoëtes*, the lamina is confined to the proximal

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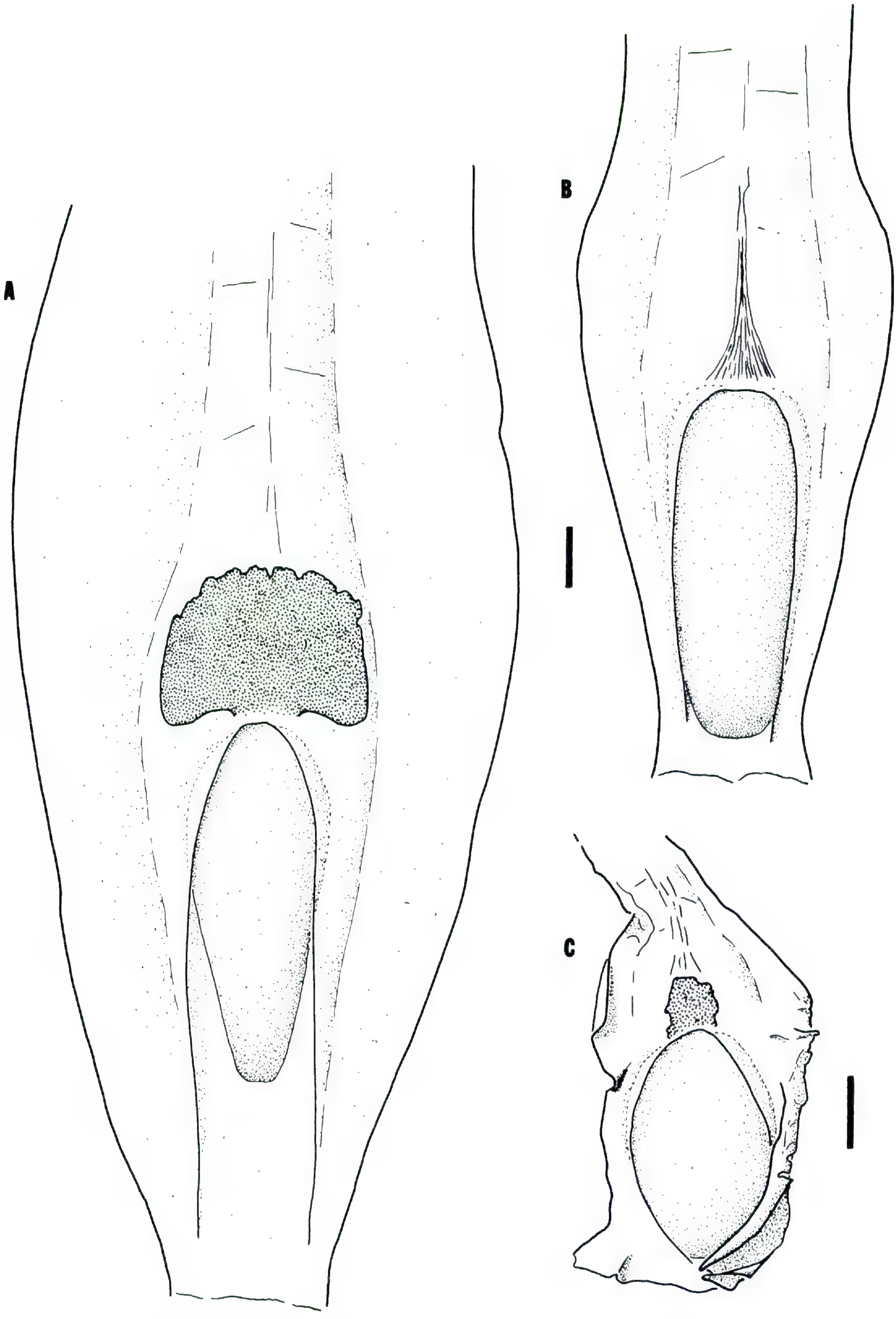

FIGURE 1. Leaf base morphology in *Isoëtes* subg. *Euphyllum*. — A. Microsporophyll of *I. gigantea* showing large labium (*Luetzelburg 298* M). — B. Microsporophyll of *I. bradei*, ligule and labium absent (*Brade 8119* AAU). — C.

portions of the leaf and a terete extension of the leaf, the subula, represents the major photosynthetic organ. The nonlaminate subula and the presence of peripheral fibrous bundles are synapomorphies that unite subg. *Isoëtes* and support its recognition as a monophyletic assemblage (Hickey, 1986a). The majority of extant *Isoëtes* species, including those previously placed in subg. (or the genus) *Stylites* (Gómez, 1980) are properly placed in subg. *Isoëtes*.

Subgenus *Euphyllum*, as currently construed, contains three modern species, *I. baculata*, *I. bradei*, and *I. gigantea*. It also appears that certain fossil taxa segregated as the genus *Isoëtites* fall within this group (Brown, 1939, 1958; Bock, 1962; Bose & Roy, 1964). While the fossil members are worldwide in distribution, the extant taxa are restricted to Brazil and the Colombia–Brazil border. This range, coupled with the plesiomorphic, grade-association nature of subg. *Euphyllum*, suggests that the extant taxa are survivors of a formerly cosmopolitan group and have survived only in isolated refugia of South America (Simpson & Haffer, 1978).

KEY TO THE SPECIES OF SUBG. *EUPHYLLUM*

1a. Sporangium elevated above leaf base; megaspores essentially saccate, proximal ridges narrow, knifelike ..... 1. *I. gigantea*
1b. Sporangium basal; megaspores baculate or tuberculate, proximal ridges as wide as or nearly as wide as high 2
  2a. Megaspores tuberculate; leaves broad, 1.8–4.5 mm wide at mid-length, the alae 3.0–5.0 mm wide at the sporangium; plants of southeastern Brazil ..... 2. *I. bradei*
  2b. Megaspores baculate; leaves narrow, 0.6–1.0 mm wide at mid-length, the alae 0.6–1.5 mm wide at the sporangium; plants of western Brazil ..... 3. *I. baculata*

1. Isoëtes gigantea U. Weber, Nova Hedwigia 63: 245. 1922. TYPE: Brazil. Rio de Janeiro: Serro dos Orgãos, Morro Assu, Hochmoor bei Isabelloca, 2,000 m, 1915, *v. Luetzelburg 6438* (lectotype, here designated M; isolectotype, M). Figures 1A, 2A, 2B, 3.

Corm globose, 25–45 mm wide, 22–35 mm high, 2-lobed; dichotomous roots arising synchronously within the continuous circumbasal fossa. Leaves 80+, dark green, laxly ascending, flattened to narrowly elliptic in cross section, 200–300 mm long, 8.0–10.0 mm wide at the base, 14.0–20.0 mm wide above the sporangium, 3.0–5.0 mm wide at mid-length, apex acute; alae light green to nearly translucent and chartaceous proximally, dark green and membranaceous distally, 5.0–6.0 mm wide at the sporangium, 1.0–2.0 mm wide at mid-length, extending to the apex; fibrous bundles absent; scales and phyllopodia absent. Sporangia obovate in face view, superficial, microsporangium walls buff, megasporangium walls light brown, 14.0–20.0 mm long, 3.0–7.0 mm wide, positioned 3.0–8.0 mm distal to the leaf base. Velum minute, 0.2–0.5 mm wide along the lateral edges of the sporangium, absent along the upper edge of the sporangium. Ligule triangular to widely deltate, delicate, the margins ephemeral, the persistent cushion dark, 4.0–5.0 mm long, 2.0–3.0 mm wide, hidden behind the more massive labium. Labium persistent, depressed ovate, cordate, entire to laciniate, buff-colored, 3.0–5.0 mm long, 5.5–7.0 mm wide. Megaspores gray, not lustrous, 590–690 ($\bar{X}$ = 616) μm diam., (verrucate to) saccate, the elements occasionally merging laterally to form meandriform rugae near the proximal ridges; equatorial ridge straight or undulate, distinct, broad, proximal ridges straight, very narrow, appearing more distinct because of the slight separation between them and the proximal ornamentation. Microspores light gray, 38.0–48.0 ($\bar{X}$ = 43) μm long, 30.0–37.0 ($\bar{X}$ = 33.0) μm wide, surface morphology of confluent papillae.

Additional specimens examined. BRAZIL. BAHIA: Quellgebiet des Rio de Contas, Minas de Contas, in einem Sumpf, Aug. 1913, *Luetzelburg 298* (M); Rio Ramalho, Feb. 1913, *Luetzelburg 15057* (M).

Isoëtes gigantea is known only from the type locality north of the city of Rio de Janeiro and from two localities in the mountains of Bahia, Brazil. While the collections of *I. gigantea* are inadequate to describe its habitat, the overall morphology suggests that it is a completely submerged aquatic, perhaps of mid-elevation (ca. 2,000 m) swamps and bogs. Fertile collections are known from February and August; there is no evidence of vegetative reproduction.

Weber's description of *I. gigantea* cites the type as "Ph. v. Lutzelburg 1915." This collection is represented by two sheets at Munich, both of which

←
Megasporophyll of *I. baculata* showing pronounced labium (*Luetzelburg 23769* M). Labium = heavily stippled regions; upper bar applies to Figures A and B, lower bar applies to Figure C, both = 2 mm.

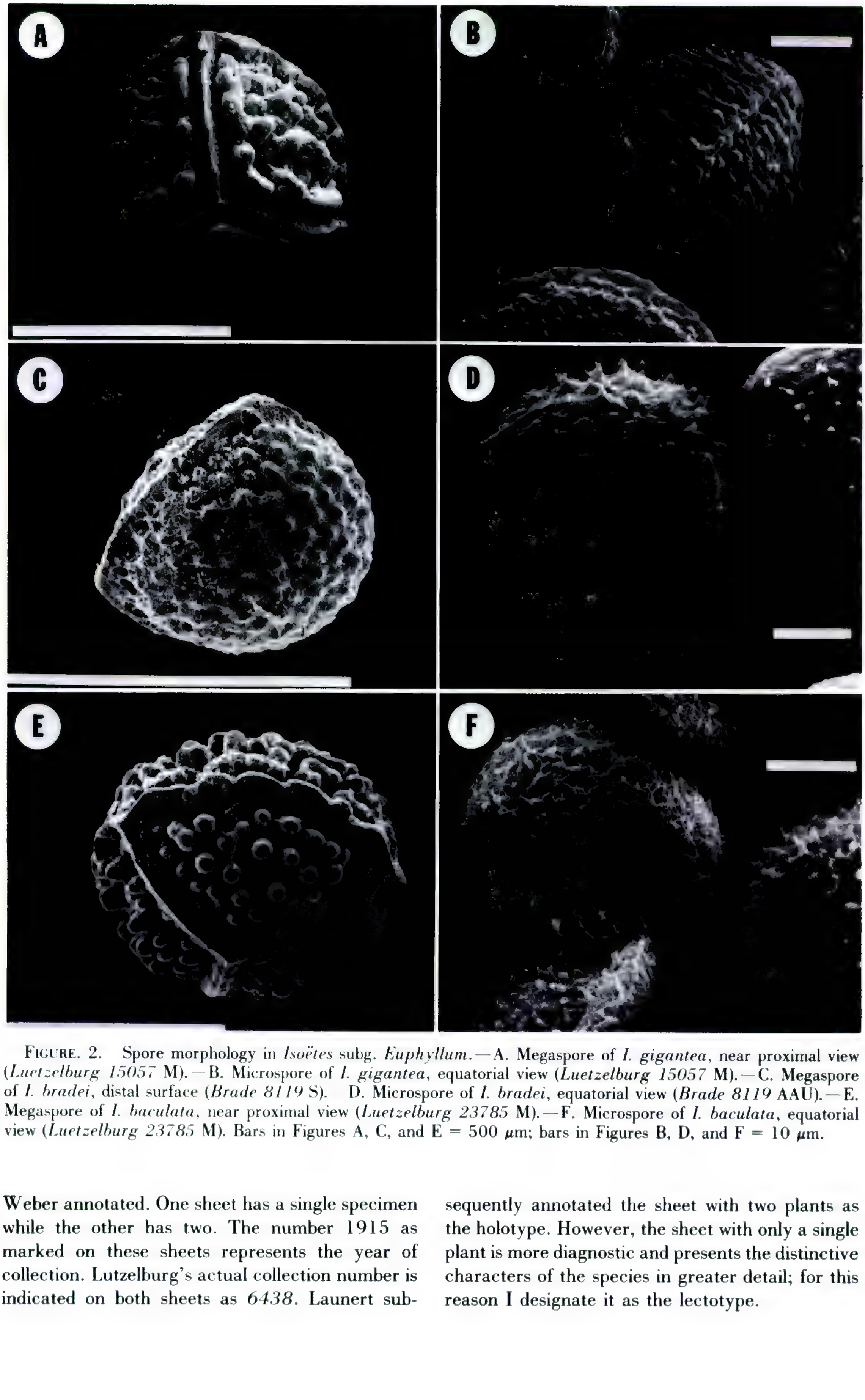

FIGURE. 2. Spore morphology in *Isoëtes* subg. *Euphyllum*.—A. Megaspore of *I. gigantea*, near proximal view (*Luetzelburg 15057* M).—B. Microspore of *I. gigantea*, equatorial view (*Luetzelburg 15057* M).—C. Megaspore of *I. bradei*, distal surface (*Brade 8119* S). D. Microspore of *I. bradei*, equatorial view (*Brade 8119* AAU).—E. Megaspore of *I. baculata*, near proximal view (*Luetzelburg 23785* M).—F. Microspore of *I. baculata*, equatorial view (*Luetzelburg 23785* M). Bars in Figures A, C, and E = 500 μm; bars in Figures B, D, and F = 10 μm.

Weber annotated. One sheet has a single specimen while the other has two. The number 1915 as marked on these sheets represents the year of collection. Lutzelburg's actual collection number is indicated on both sheets as *6438*. Launert subsequently annotated the sheet with two plants as the holotype. However, the sheet with only a single plant is more diagnostic and presents the distinctive characters of the species in greater detail; for this reason I designate it as the lectotype.

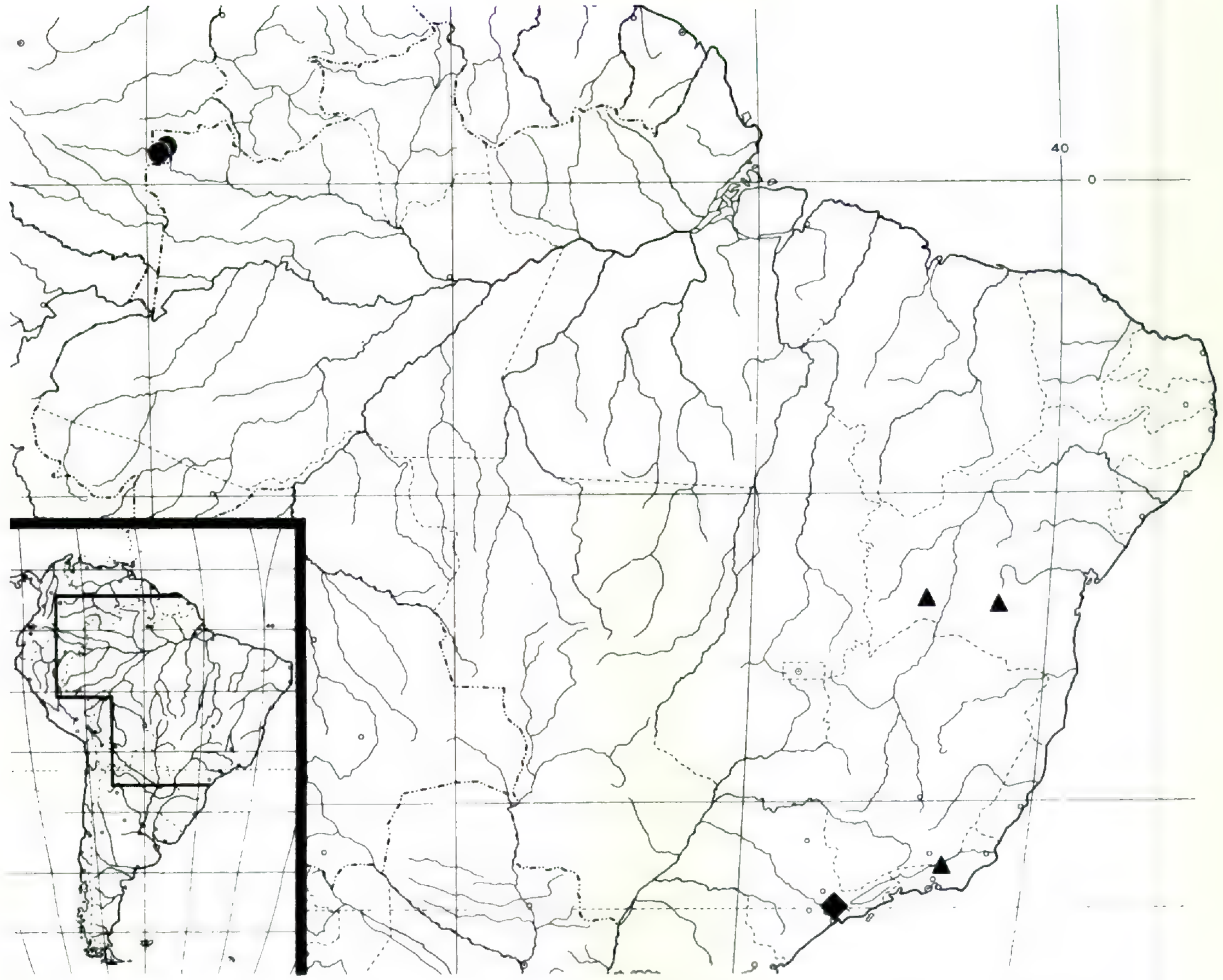

FIGURE 3. Collection sites of *I. gigantea* (triangles), *I. bradei* (diamond), and *I. baculata* (dots).

Isoëtes gigantea is one of the most easily recognized species of *Isoëtes*. The broadly laminate leaves, massive sporangia, which are virtually superficial on the leaf surface, and saccate megaspores are immediately distinctive. The large, persistent labium and the narrow, knifelike proximal ridges are also characteristic.

The saccate megaspores and the microspores with confluent papillae are uniquely derived character states (= autapomorphies) and do not provide evidence of relationships. Ancestral states, such as a completely laminate leaf, a lack of scale leaves and fibrous bundles, a poorly developed velum, and a large labium, suggest a grade level relationship with *I. baculata* and *I. bradei*.

2. Isoëtes bradei Herter, Rev. Sudamer. Bot. 8: 19. 1949. TYPE: Brazil. São Paulo: Villa Emma, Rio Mooca, 1921, *Brade 8119* (holotype, G; isotypes, AAU, S, UC, US). Figures 1B, 2C, 2D, 3.

Corm ellipsoid, ca. 20 mm wide, ca. 10 mm high, 3(?)-lobed; dichotomous roots arising synchronously within the continuous circumbasal fossa(e). Leaves 60–100+, medium to dark green, flexuous, flattened to elliptic in cross section, 630–700 mm long, 5.0–8.0 mm wide at the base, 8.0–15.0 mm wide above the sporangium, 1.8–4.5 mm wide at mid-length, apex attenuate; alae medium to dark green, membranaceous, 3.0–5.0 mm wide at the sporangium, extending to the apex; fibrous bundles absent; scales and phyllopodia absent. Sporangium narrowly obovate in face view, superficial to slightly embedded, the walls tan to light brown, concolorous, 10.0–15.0 mm long, 4.0–5.0 mm wide, basal. Velum minute, 0.0–0.5 mm wide along the lateral edges of the sporangium, absent along the upper edge of the sporangium. Ligule not seen. Labium ephemeral, frequently represented by a widely ovate brown fragment, 2+ mm long, 2.2 mm wide. Megaspores white to gray when dry, dark when wet, slightly lustrous, 500–660 ($\bar{X}$ = 609) μm diam., tuberculate; equatorial ridge undulate, much higher than wide, proximal ridges straight, distinct, much higher than wide; occasional dumbbell spores and very small (350–360

μm) spores produced. Microspores light gray, 40.0–51.3 ($\bar{X}$ = 45) μm long, 32.5–38.8 ($\bar{X}$ = 35) μm wide, echinate or the echinae broken off leaving a papillate surface.

Additional specimen examined. BRAZIL. SÃO PAULO: Río Mooca, Villa Emma, *Brade 7946* (SP).

No ecological or phenological data accompany any of the collections but in the protologue Herter stated that the plant is submersed. This statement is supported by the general morphology and habit of the plants; that is, they are extremely large, lack scales and phyllopodia, and have long flexuous leaves lacking supporting fibrous bundles. There is no evidence of vegetative reproduction.

Isoëtes bradei is one of several poorly known, low- to medium-elevation species from Brazil. It is known only from the two Brade collections made at the Villa Emma population in São Paulo which, according to the label data on the isotype (AAU), has been completely destroyed. Despite the limited amount of material available, there is no doubt that *I. bradei* is distinct. The broadly alate leaves coupled with the tuberculate megaspores are characteristic. The presence of small, and occasionally dumbbell shaped spores is interesting in that no accompanying microspore abnormalities have been observed. Such observations suggest that an ecological stress may have resulted in abnormal megasporogenesis in the type specimen.

3. Isoëtes baculata Hickey & Fuchs in Hickey, Syst. Bot. 11: 310. 1986. TYPE: Brazil. Amazonas (Uaupés): im fluss auf d. Colombianisches Seite, 28 Nov. 1916, *Luetzelburg 23785* (holotype, M). Figures 1C, 2E, 2F, 3.

Corm globose, 13–18 mm diam., 2-lobed; dichotomous roots arising synchronously within the continuous circumbasal fossa. Leaves 26–29, light green, flexuous, flattened to elliptic in cross section, 600–650 mm long, 5.0–8.0 mm wide at the base, 0.6–1.0 mm wide at mid-length, apex attenuate; alae light green to nearly colorless and chartaceous proximally, light green and membranaceous distally, 0.6–1.5 mm wide at the sporangium, extending to the apex as two minute lateral ridges; fibrous bundles absent; scales and phyllopodia absent. Sporangium elliptic in face view, embedded, the walls pale tan, concolorous, 5.5–7.0 mm long, 2.5–4.5 mm wide, basal. Velum minute, 0–1.5 mm wide along the lateral edges of the sporangium, absent along the upper edge of the sporangium. Ligule margins delicate, ephemeral, the persistent cushion tan, membranaceous, deltate to widely deltate, cordate, 1.4 mm long, 1.8 mm wide. Labium partially persistent, widely ovate to very widely ovate, entire to erose, tan, 0.7–1.6 mm long, 1.3–1.6 mm wide. Megaspores light gray, not lustrous, (470–)580–730 ($\bar{X}$ = 667) μm diam., baculate to subverrucate, the bacula isolated or fused into groups of two or three, 60–80 μm in height, 30–40 μm wide; equatorial ridge straight or undulate, 2 to 3 times as high as wide, proximal ridges straight, distinct, as wide as or slightly wider than high. Microspores light gray, 35.0–43.0 ($\bar{X}$ = 39.0) μm long, 27.0–34.0 ($\bar{X}$ = 31.0) μm wide, echinate or smooth, their surface covered with a fine, fibrous perispore.

Additional specimen examined. COLOMBIA. VAUPÉS: Uapes [sic], submersus auf Colombianisch Ufer, 28 Nov. 1918, *Luetzelburg 23769* (M).

Isoëtes baculata is, as far as is known, confined to the Río Vaupés amd Río Negro drainages along the Colombia–Brazil border. According to label data it is a submerged aquatic; this is substantiated by the lax, flexuous habit of its leaves. Both collections of this species were made in November and both have abundant megaspores and microspores. There is no evidence of vegetative reproduction.

Isoëtes baculata is readily identified by its long flexuous leaves, which are narrowly laminate for their entire length, and by the large, baculate megaspores. There is a distinct phenetic relationship between *I. baculata* and *I. panamensis* Maxon, particularly in the morphological similarity of megaspores, micropsores, velum, and labium. Many of these similarities, however, appear to be the result of convergence or are the result of the retention of plesiomorphic character states in the otherwise derived *I. panamensis* (Hickey, 1985). Convergence in the echinate morphology of the microspores is obvious when they are viewed at high magnifications: the perispore of *I. panamensis* microspores is smooth and lacks the loosely fibrous morphology of *I. baculata*. Preliminary phylogenetic analyses on the genus (Hickey, 1985, 1986b) also indicate that the tuberculate surface morphology is plesiomorphic within subg. *Isoëtes* and that the baculate megaspores of *I. baculata* are convergent with respect to *I. panamensis*. The lack of velum coverage and the large labia are plesiomorphic states in each taxon and cannot be used as indicators of phylogenetic relationship.

In the absence of obvious synapomorphies, I have included *I. baculata* in subg. *Euphyllum*. It deviates most significantly from *I. gigantea* and *I. bradei* in having poorly developed alae and partially embedded sporangia. Both *I. gigantea* and

I. bradei have sporophyll bases widest above the sporangium with a subtruncate narrowing of the leaf above the labium; *I. baculata* has leaves widest at or below the sporangium with a gradual reduction in leaf base width distally. In this regard, *I. baculata* is more similar to members of the subg. *Isoëtes*.

Terminology: The various terms for organs and their character states are discussed in Hickey (1985, and 1986a); megaspore morphology follows the terminology presented in Hickey (1986b). Two-dimensional shape characterizations for the ligule, labium, and sporangium follow the terminology of Radford et al. (1972).

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TWO NEW SPECIES OF *CNEMIDARIA* (CYATHEACEAE) FROM PANAMA[1]

Robbin C. Moran[2]

ABSTRACT

Cnemidaria suprastrigosa and *Cnemidaria varians* are named as new species in the fern family Cyatheaceae.

In 1974, Robert G. Stolze of the Field Museum of Natural History, Chicago, published a monograph of *Cnemidaria* based on a study of nearly 2,000 specimens from 17 herbaria. He was helped and encouraged throughout his study by Rolla and Alice Tryon, who provided the original impetus for his research as well as many other studies in the Cyatheaceae. Since the publication of Stolze's excellent monograph, new collections have turned up two new species of *Cnemidaria* in addition to the 23 species recognized by Stolze (1974). Both are from Panama.

Cnemidaria suprastrigosa R. C. Moran, sp. nov. TYPE: Panama. Veraguas: Cerro Tute, Santa Fé, ridge up from former Escuela Agrícola, 1,000–1,300 m, *Hamilton & Dressler 3049* (holotype, MO). Figure 1e.

Lamina adaxialiter strigosa, apice pinnatifida, pinnis distantiae ad costam ca. ⅔ incisis; venis basalibus junctis; rhachidi exalata; soris medianis; indusiis semicircularibus.

Stem not seen; leaves ca. 1.5 × 0.3 m, the veins pubescent adaxially, with hairs 0.2–0.4 mm, subulate, strigose, scattered, the apex evenly tapered, pinnatifid; petiole lacking spines, with only a few scattered hairs and scales; rachis nonalate or slightly winged below the bases of the distal pinnae, the abaxial surface pubescent, the hairs hyaline, retrorsely strigose; pinnae sessile, cut ca. ⅔ to the costa; costae scaly and pubescent abaxially, the scales scattered, brown, amorphous, the adaxial surface pubescent; veins 1–2-forked, the basal ones anastomosing to form costal areoles; sori medial; indusia semicircular, positioned on the costular side of the receptacle.

This species differs from all others in the genus by its adaxial pubescence along the veins (Fig. 1e). It was formerly thought that the glabrous adaxial surface of the lamina was one of the distinctions between *Cnemidaria* and *Cyathea*.

Cnemidaria suprastrigosa is known only from the type collection.

Cnemidaria varians R. C. Moran, sp. nov. TYPE: Panama. Panamá: Cerro Jefe, 1,000 m, *Valdespino & Aranda 139* (holotype, MO; isotypes, UC, PMA not seen). Figure 1a–d.

Lamina adaxialiter glabra, abaxialiter glandibus punctatis rubellis munita, apice pinnatifida attenuata vel abrupte reducta; pinnis integris vel distantiae ad costam ⅛–¼ incisis, paribus basalibus reductis; rhachidi ubique alata; soris medianis vel supramedianis; indusiis circularibus vel semicircularibus.

Stem to 90 cm; leaves to 1.4 × 0.32 m, lanceolate, the abaxial surface punctate with reddish glands, the apex attenuate or abruptly reduced, pinnatifid; petiole base smooth, the scales bicolorous; rachis alate throughout, the wing to 2 mm, glabrous to sparsely pubescent abaxially, brown; pinnae 12–15 × 2–2.3 cm, sessile or the basal ones stalked, entire or cut ⅛–¼ to the costa, the 2 lowermost pairs reduced, ca. half the length of the longest medial pinnae; costae glabrous to sparsely pubescent abaxially, sparsely scaly, the scales dark; veins not branched, mostly anastomosing, occasionally free; sori medial to inframedial; indusia circular, completely surrounding the base of the receptacle, or semicircular and positioned on the costular side of the receptacle.

Paratypes. PANAMA. DARIÉN: Panama/Colombia border, Parque Nacional del Darién, near gold mine at headwaters of N branch of Río Pucuro, slopes of Cerro Tacarcuna, ca. 6 km N of Cerro Mali, 1,300 1,500 m,

[1] I thank Robert G. Stolze for helpful comments on the manuscript.

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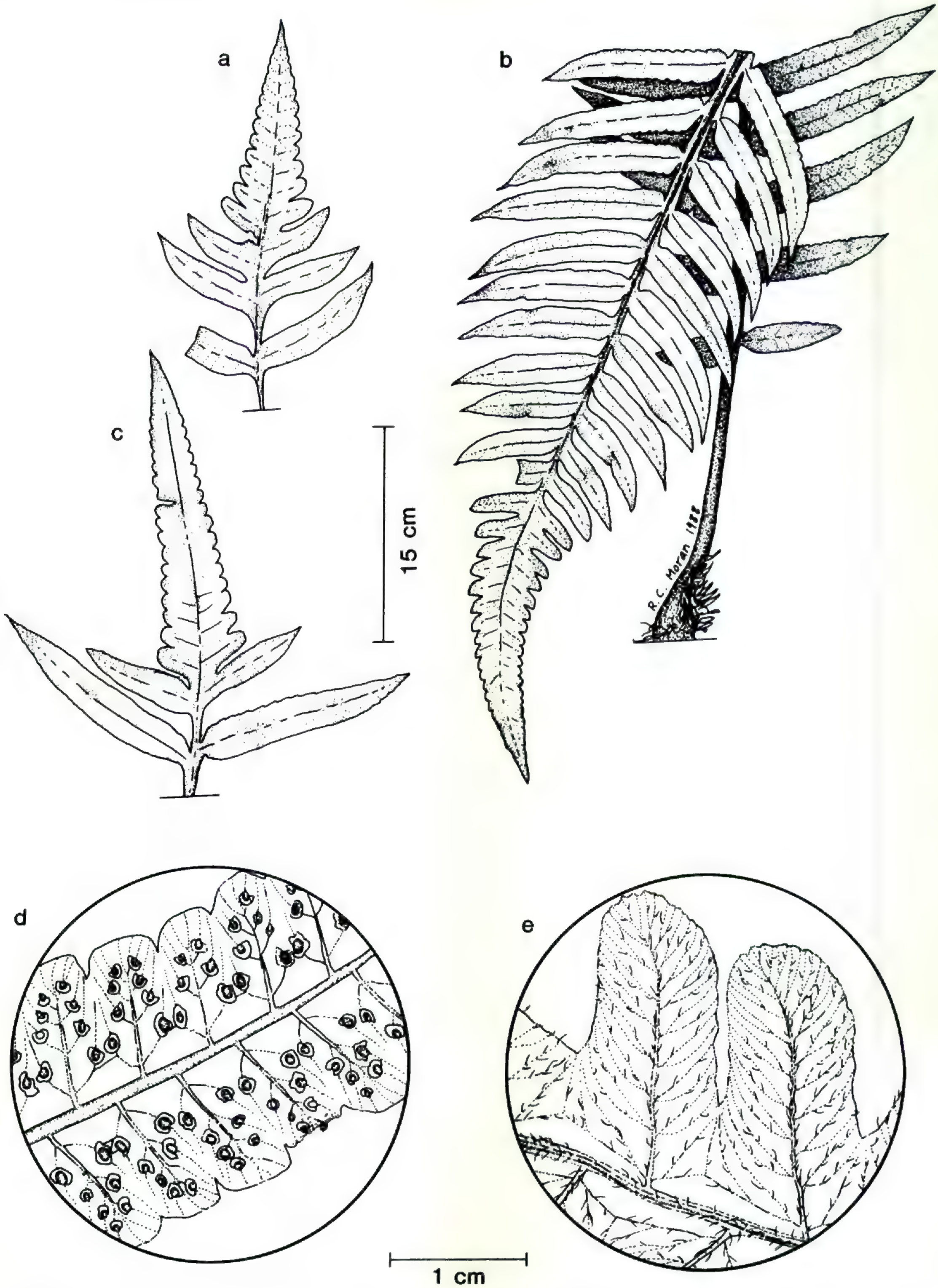

FIGURE 1. a–d. *Cnemidaria varians*.—a–c. Variation in shape of the leaf apex.—d. Abaxial surface of leaf.—e. *Cnemidaria suprastrigosa*, adaxial leaf surface showing strigose hairs. a. *Mori & Kallunki 3798* (MO). b, c, d. *Valdespino & Aranda 139* (UC). e. *Hamilton & Dressler 3049* (MO).

de Nevers et al. 116531 (COL, MO, PMA, UC). PANAMÁ: Cerro Jefe, along trail on ridge running NE from summit, cloud forest dominated by *Clusia* spp. and *Colpothrinax cookii*, ca. 1,000 m, *Mori & Kallunki 3798* (MO).

This species is extremely variable in characters that are usually constant in other species of *Cnemidaria*, thus the specific epithet *varians*. For example, the shape of the apex, even on the same plant, varies from evenly tapered (Fig. 1b) to abruptly contracted (Fig. 1c); intermediates are known (Fig. 1a). The basal veins are anastomosing or are free (Fig. 1d). The type collection had a stem 90 cm long, but the Darién collection was described as a "terrestrial rosette with no stem." This variation in several characters suggests hybrid origin, but I cannot find suitable parent species. The spores are normal, i.e., not aborted.

This new species might be confused with *Cnemidaria decurrens* (Liebm.) R. Tryon because both have alate rachises and entire or shallowly lobed pinnae. The new species differs, however, from *C. decurrens* by its spineless petiole, reduced basal pinnae, and minute, round, reddish glands on the abaxial surface of the lamina. *Cnemidaria decurrens* is known from southern Mexico to Honduras, whereas *C. varians* is endemic to eastern Panama.

This new species also resembles *C. glandulosa* Stolze because both have relatively small leaves, pinnae that are not deeply lobed, and minute reddish glands on the abaxial surface of the lamina. *Cnemidaria varians* differs, however, from *C. glandulosa* by having alate rachis, shallowly lobed pinnae, dark costal scales, unbranched veins, basal veins that frequently anastomose, and sometimes fully circular indusia that completely surround the base of the receptacle. Both species are known only from Panama.

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PTERIDOPHYTES OF THE VENEZUELAN GUAYANA: NEW SPECIES

Alan R. Smith[1]

Abstract

Studies on the pteridophytes of the Venezuelan Guayana have resulted in the description of the following 31 new species: *Asplenium chimantae*, *A. cowanii* (Aspleniaceae); *Cyathea liesneri*, *C. neblinae*, *C. praeceps* (Cyatheaceae); *Sticherus tepuiensis* (Gleicheniaceae); *Ceradenia arthrothrix*, *C. microcystis*, *Grammitis liesneri*, *G. peritimundi*, *G. plicata*, *G. sinuosa* (Grammitidaceae); *Pleopeltis repanda* (Polypodiaceae); *Adiantum nudum*, *A. amazonicum*, *Doryopteris cyclophylla*, *D. davidsei* (Pteridaceae); *Selaginella albolineata*, *S. arrecta*, *S. beitelii*, *S. breweriana*, *S. cyclophylla*, *S. imbricans*, *S. marahuacae*, *S. neblinae*, *S. pubens*, *S. sobolifera*, *S. thysanophylla*, *S. velutina*, *S. versatilis* (Selaginellaceae); *Thelypteris peradenia* (Thelypteridaceae). In addition, new combinations are made for the following six taxa: *Salpichlaena lomarioidea* (Blechnaceae); *Cyathea macrosora* var. *reginae*, *C. macrosora* var. *vaupensis*, *C. thysanolepis*, *Grammitis blanchetii*, and *Sticherus tomentosus*.

Aspleniaceae

Asplenium chimantae A. R. Smith, sp. nov. TYPE: Venezuela. Bolívar: Dtto. Piar, Macizo del Chimantá, sector centro-noreste del Chimantá-tepuí, cabeceras orientales del Caño Chimantá, alrededor del comienzo E del Cañón recto del Río Chimantá superior, 5°18′N, 62°09′W, ca. 2,000 m, 26–29 Jan. 1983, *Huber & Steyermark 6927* (holotype, UC; isotypes, AAU, VEN not seen). Figure 1 A–C.

Ex affinitate *A. dissecti* Sw., pinnis latioribus, paucioribus, minus incisis distinctum; ab *A. serra* Langsd. & Fischer lamina subtiliore, textura membranacea, paleis rhizomatis attenuatioribus ad apicem filiformem et luminibus palearum majoribus hyalinioribus differt.

Rhizome short-creeping, densely scaly; rhizome scales spreading, blackish, lanceolate with a long uniseriate tip, clathrate, up to 8 × 0.5 mm; fronds clustered, to ca. 35 cm long; stipe to ca. 12 cm × 1 mm, blackish or atropurpureous, shining, glabrescent or with a few filiform scales; rachis similarly colored, bearing scattered filiform scales up to 2 mm long, 1–3 cells wide at the base; lamina ovate, 1-pinnate with a pinnatifid apex; pinnae to ca. 10 pairs, ± bilaterally symmetrical or with the basiscopic side slightly excised, to 5 × 1.3 cm, broadly cuneate or rounded at the base, attenuate at the tip, margins serrately or biserrately incised up to half the distance to the costa; veins simple or 1-forked, strongly ascending at ca. 20° from the costa; lamina glabrous on both sides or abaxially with inconspicuous, ± appressed, septate hairs to 0.3 mm; sori borne near the base of the veins or at vein forks, nearer the costa than the margin, mostly 2–5 mm long, with a linear or oblong white or gray indusium ca. 0.7 mm wide.

Paratype. Same locality as type, *Steyermark, Huber & Carreño 128211* (VEN).

This species is perhaps most closely related to *A. dissectum* Sw., known from the Greater Antilles and southern Mexico to Ecuador, Venezuela, and southern Brazil, but the new species differs in the wider, less incised pinnae in fewer pairs. It is also related to *A. serra* Langsd. & Fischer, from which it differs in the more delicate, thin-textured lamina and more attenuate rhizome scales with larger and clearer lumina and long-filiform tip. The type was described as growing in deep grottoes.

Asplenium cowanii A. R. Smith, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Serranía Parú, Río Ventuari, dry crevices of cliff, talus forest, 1,800 m, 12 Feb. 1951, *Cowan & Wurdack 31393* (holotype, US). Figure 1D–E.

A. repenti Hook. primo adspectu maxime simile, sed rhizomate breviter repenti vel suberecto, frondibus fasciculatis, stipite et rhachidi rubrobrunneis vel atropurpureis.

Rhizome short-creeping to suberect; rhizome scales dark reddish brown, lanceolate with a uniseriate tip, clathrate, ca. 2–3 × 0.3 mm; fronds densely clustered, to ca. 6 cm long; stipe to 1.5 cm × 0.2 mm, reddish brown to atropurpureous,

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shining, glabrous or with a few filiform scales 1–3 cells wide; rachis similarly colored, glabrous; lamina pinnate-pinnatifid to barely 2-pinnate with a pinnatifid or cleft apical segment; pinnae 5–10 pairs, to 6 × 4 mm, with at most 1 pair of lateral pinnules and a terminal segment, the lateral ones bifid or trifid, the terminal 3–6-cleft; one vein per ultimate lobe; lamina glabrous on both sides; sori 1–3 per pinna, the indusium oblong to semicircular, 1 × 0.4 mm, brownish.

This very distinct new species, known only from the type, is most closely related to *A. repens* Hook., from Ecuador and Peru, from which it differs by the short-creeping or suberect rhizome (vs. long-creeping in *A. repens*) with fasciculate fronds and by the reddish brown or atropurpureous (vs. greenish to tan) stipe and rachis. In laminar dissection, the two species are very similar.

BLECHNACEAE

Salpichlaena lomarioidea (Baker) A. R. Smith, comb. nov. *Blechnum volubile* Kaulf. var. *lomarioidea* Baker in C. Martius, Fl. Bras. 1(2): 428. 1870.

Distribution. Guianas to Peru.

Specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: 15 km SE de San Fernando de Atabapo, *Stergios et al. 11605* (UC); Dpto. Río Negro, Neblina Base Camp, *Beitel 85222* (UC). COLOMBIA. VICHADA: ca. 25 km E of Cumaribo on road between Las Gaviotas and Santa Rita, *Davidse 5315* (MO). PERU. LORETO: *McDaniel et al. 21515* (MO), *Klug 1126* (MO), *Moran 3672* (UC).

CYATHEACEAE

Cyathea macrosora (Baker) Domin var. **reginae** (Wind.) A. R. Smith, comb. nov. *Sphaeropteris macrosora* (Baker) Wind. var. *reginae* Wind., Bradea 1: 374. 1973.

Cyathea macrosora (Baker) Domin var. **vaupensis** (Wind.) A. R. Smith, comb. nov. *Sphaeropteris macrosora* (Baker) Wind. var. *vaupensis* Wind., Bradea 1: 374. 1973.

Cyathea thysanolepis (Barrington) A. R. Smith, comb. et stat. nov. *Trichipteris demissa* (C. Morton) R. Tryon var. *thysanolepis* Barrington, Rhodora 78: 1. 1976.

Cyathea liesneri A. R. Smith, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dpto. Río Negro, Cerro Aracamuni, summit, Popa camp, 01°26′N, 65°47′W, 1,550 m, 16 Oct. 1987, in dwarf forest, *Liesner & Delascio 21964* (holotype, UC 2 sheets; isotype, MO not seen). Figure 2K–N.

Probabiliter *C. williamsii* (Maxon) Domin et *C. cyclodio* (R. Tryon) Lellinger affinis, ab ambabus imprimis differt lamina bipinnata (vs. 1-pinnata), paleis stipitis congestis, longioribus, ovatioribus, minus manifeste bicoloribus, paraphysibus densioribus, paleis costarum ovatioribus, brunneis, nitentibus.

Rhizome not known, plants probably acaulescent or with a short trunk; fronds ca. 1.5–2.0 m; stipe lacking spines, dark brown to atropurpureous, ca. 90 × 1.2 cm, the basal third with spreading, lanceolate scales to 1.5 cm × 2 mm, these with a dark brown to blackish central portion and narrow tan to whitish margins, cells toward the margin flaring outward and ending in short cilia; stipe scurf (microscales) seemingly lacking or sparse; rachis tan, becoming alate distally; lamina 2-pinnate at the base, pinnate-pinnatifid distally, the pinnae progressively shortened and less divided, the lamina ultimately ending in a pinnatifid apex; pinnae nonarticulate, largest ones to ca. 35 × 9 cm, alate and pinnatifid distally; pinnules elliptic, to 5 × 1.2 cm, entire or crenulate (especially toward the tip), narrowed at the base, sessile or becoming adnate distally; veins free, main ones from costules with 1 or 2 pairs of strongly ascending veinlets, these running ± parallel to margin, slightly raised and readily visible on both sides; costules lacking hairs abaxially, with scattered, shiny, brown, ovate-lanceolate scales, these uniseriate at the tip, the margins with ascending, ciliate teeth; sori in a single row on each side of the costules, nonindusiate, borne on the veins ca. ⅓–½ the way toward the margin, with persistent, rather dense, brownish, filiform paraphyses equal to or slightly exceeding the sporangia; spores whitish, strongly 3-lobed.

This species is probably most closely related to *C. williamsii* (Maxon) Domin and *C. cyclodium* (R. Tryon) Lellinger but differs from both in the bipinnate lamina and longer, more numerous, and less sharply bicolorous stipe scales, denser paraphyses, and more ovate, shiny brown costal scales. Many of the spores seem collapsed, which might be indicative of a hybrid origin, but I can find no other species from the area that might serve as the other parent. The distinctive blade dissection is sufficient to allow recognition of *C. liesneri*.

Cyathea neblinae A. R. Smith, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dpto. Río Negro, 0–1 km E of Cerro de la Neblina Base Camp on Río Mawarinuma, 0°50′N, 66°10′W, 140 m, 9 Feb. 1984, on steep

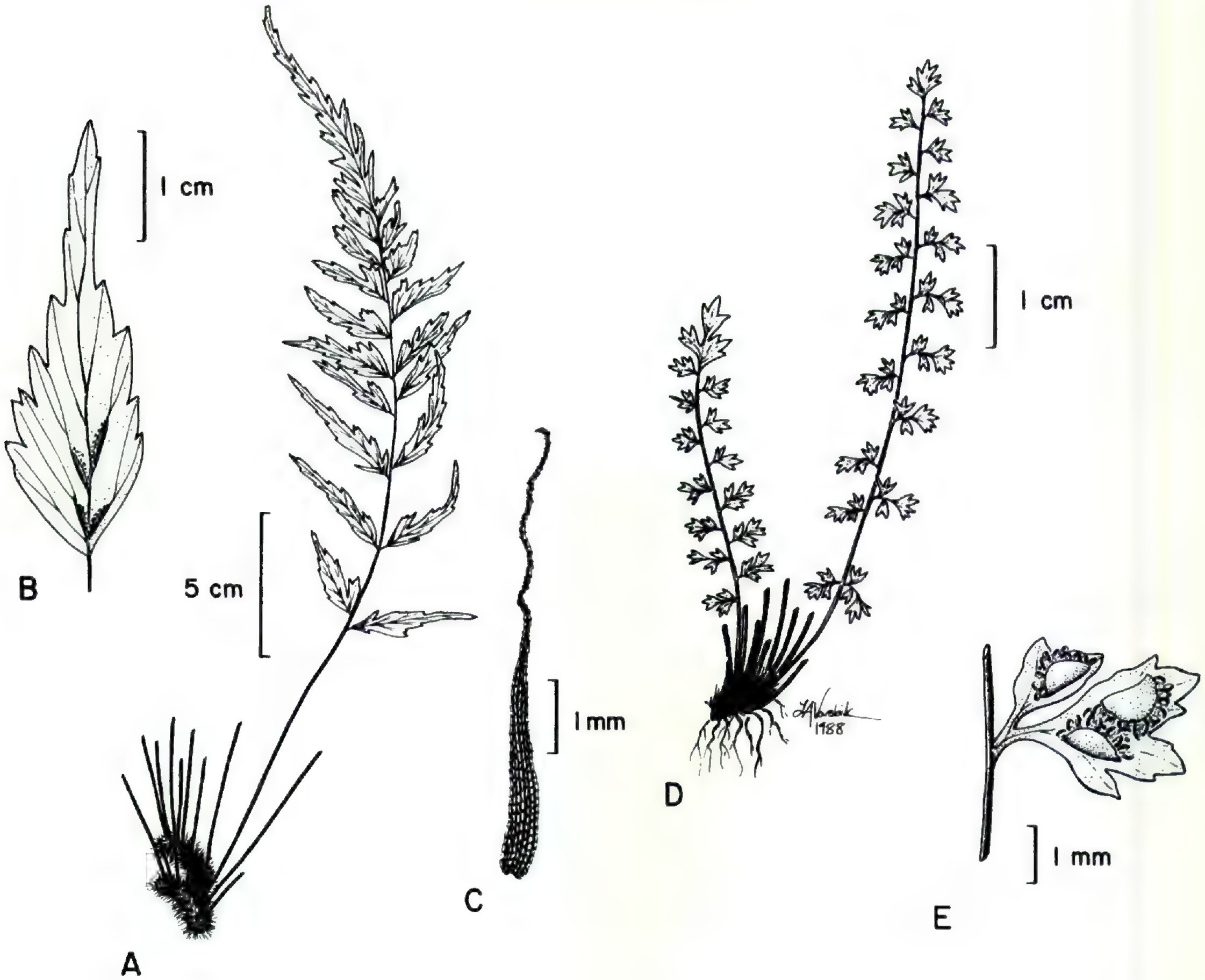

FIGURE 1. New species of *Asplenium*. A–C. *Asplenium chimantae, Huber & Steyermark 6927*, UC.—A. Habit.—B. Pinna, abaxial surface.—C. Scales from rhizome apex. D–E. *Asplenium cowanii, Cowan & Wurdack 31393*, US.—D. Habit.—E. Pinna, abaxial surface.

moss-covered bank, *Liesner & Funk 15781* (holotype, UC; isotype, MO not seen). Figure 2F–J.

Differt a *C. pungenti* (Willd.) Domin trunco minus quam 30 cm longo, frondibus plerumque 0.5–1.0 m longis, pinnato-pinnatifidis vel bipinnatis, pinnulis integris vel crenulatis, segmentis obliquioribus, falcatis, axibus abaxialiter epilosis, paleis costarum sparsis.

Rhizome erect, caudex 7–30 × ca. 1–2(–2.5) cm; fronds 50–100(–150) cm; stipe with a few spines, 8–30(–60) cm × 2–10 mm, brown to atropurpureous, with lanceolate scales 5–10 mm at the base, these strongly and sharply bicolorous with a dark brown central portion and whitish margins, the marginal cells flaring outward and ending in short cilia; stipe scurf of sparse brownish microscales; lamina chartaceous, drying dark, pinnate-pinnatifid to bipinnate or less often 2-pinnate-pinnatifid (if the latter then with only 1–4 pairs of lower pinnae pinnate-pinnatifid), apex gradually reduced, not pinnalike; pinnae nonarticulate, largest ones 5–15(–30) × 1.5–4(–13) cm, segments or pinnules entire to pinnatifid; ultimate segments oblique, falcate, acutish at the tip; costae and costules lacking hairs abaxially, with scattered whitish to tan, bullate scales ca. 0.5–1.5 mm, costae winged; veins mostly simple in pinnatifid pinnae, often forked in pinnate pinnae; sori nonindusiate, medial on the veins, with paraphyses much shorter than the sporangia.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: same general locality as type, 17 July 1984, river bank with nearly pure bamboo stand, *Davidse & Miller 27456* (UC); same general locality, 25–26 Nov. 1984, *Liesner 17274* (UC); same locality, 9 Feb. 1984, *Liesner 15798* (UC); same general locality, 160 m, 26 Nov. 1984, *Kral 71836* (UC); same general locality, 1.5 km E of Base Camp, 2–3 Dec. 1984, *Liesner 17419* (UC); same general locality, 25 Nov. 1984, *Croat 59303* (UC); same general locality, 26 Nov. 1984, *Bell 310* (UC); same general locality, 3 Dec. 1984, *Croat 59596* (UC).

This species is most closely related to *C. pun-*

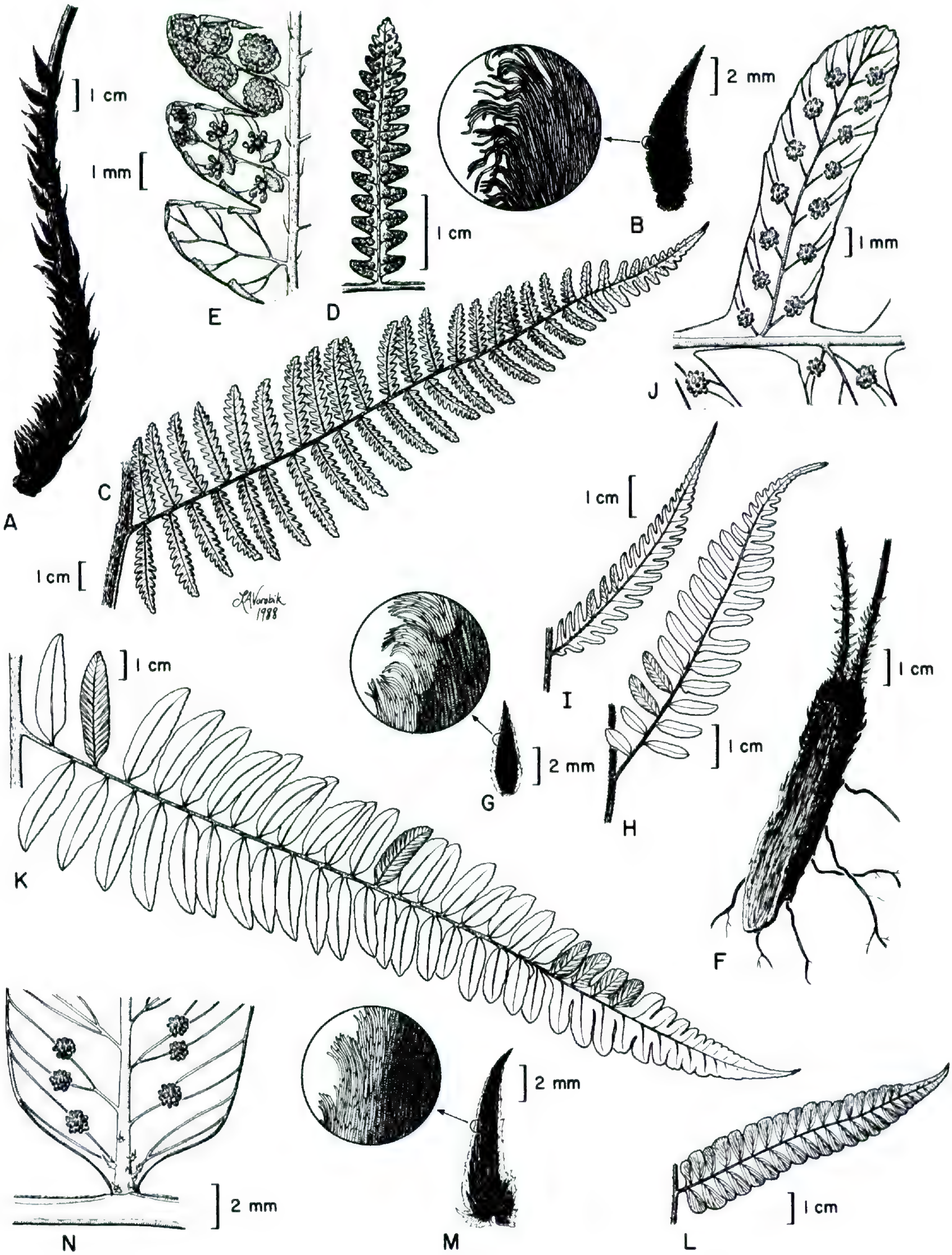

FIGURE 2. New species of *Cyathea*. A–E. *Cyathea praeceps, Stein et al. 1655*, UC.—A. Stipe base.—B. Stipe scale, with detail of margin.—C. Pinna.—D. Pinnule.—E. Abaxial surface of ultimate segments, showing sori and indusia. F–J. *Cyathea neblinae, Liesner & Funk 15781*, UC.—F. Rhizome and stipe bases.—G. Stipe scales, with detail of margin.—H. Proximal pinna.—I. Distal pinna.—J. Ultimate segments, showing sori and venation. K–N. *Cyathea liesneri, Liesner & Delascio 21964*, UC.—K. Proximal pinna.—L. Distal pinna.—M. Costal scales, with detail of margin.—N. Base pinna, showing sori and venation.

gens (Willd.) Domin, with which it shares very similar bicolorous stipe-base scales, nonindusiate sori with short paraphyses, and mostly unbranched veins. Barrington has determined two of the collections cited, including the holotype, as young fertile plants of that species as *Trichipteris procera* (Willd.) R. Tryon. *Cyathea neblinae* differs from *C. pungens* in the smaller size of the plants with fronds mostly 0.5–1.0 m; the short, thin trunk less than 30 cm; the lamina commonly merely pinnate-pinnatifid or bipinnate with entire to crenulate pinnules; the more oblique and falcate ultimate segments (segments only slightly oblique, nonfalcate, and rounded at the tip in *C. pungens*); the essentially hairless, often darkened axes abaxially; and in the rather sparse costal scales. The last three paratypes cited have 2–4 lowermost pairs of pinnae pinnate-pinnatifid before the pinnae become merely deeply pinnatifid.

All of the collections seen are from the base of Cerro de la Neblina.

Cyathea praeceps A. R. Smith, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dpto. Río Negro, Cerro de la Neblina, 6.5 km SSW of base camp, southern extension of range, 0°47′N, 66°11′W, 1,600 m, 18 Apr. 1984, dense rain forest with Euterpe palms, *Clusia*, and Cyclanthaceae, *Stein, Thompson & Gentry 1655* (holotype, UC; isotype, MO not seen). Figure 2A–E.

A *C. platylepis* (Hook.) Domin indusiis hemitelioidiis, axibus abaxialiter glabris vel sparsim pilosis, frondibus monomorphis differt.

Weakly arborescent, with trunk ca. 50 cm; fronds ca. 1–1.4 m long; stipe lacking spines or muricate, brownish to atropurpureous, at the base with dense, persistent, lustrous ovate scales to 25 × 6 mm, with a dark brown central portion and with slightly and gradually lighter brownish margins, cells toward the margin flaring outward and ending in tan to whitish cilia; stipe scurf lacking; lamina subcoriaceous, 2-pinnate-pinnatifid to barely 3-pinnate; pinnae nonarticulate, the largest ones up to ca. 30 cm; pinnules pinnatifid to barely pinnate, largest ones 3.5–6 × 0.6–1.7 cm, sessile or the largest stalked to 2 mm; segments entire to crenulate; costae abaxially lacking hairs or sparsely long-hairy, bearing scattered, brownish, ovate scales; veins forked at the sori; sori inframedial to medial, at the base with a small, tan, hemitelioid indusium not surrounding the sorus, also with tan, filiform paraphyses equal to or exceeding the sporangia; spores beige.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dpto. Atabapo, Cerro de Marahuaca, between Río Yameduaka arriba and base of cliff, 3°38′N, 65°28′W, 1,225 m, 20 Feb. 1985, *Liesner 17742* (UC); Dpto. Río Negro, Cerro de la Neblina, Camp 3, NW Plateau 13.5 km ENE of Base Camp, 0°54′N, 66°04′W, *Liesner 16082* (UC); Dpto. Atabapo, Cerro Marahuaca, SE slopes, below Salto Los Monos, 3°35′N, 65°23′W, 1,500–1,600 m, 20 Oct. 1988, *Liesner 25120* (UC).

The second paratype cited was determined by R. Tryon in 1986 as "*Cyathea*—very close to or a variant of *C. platylepis*." This may indeed be its closest relative, but it differs from that in the hemitelioid indusium, general lack of hairs on the axes abaxially, and monomorphic fronds.

The first paratype cited contains the following note, which suggests the specific epithet: "Please forgive condition [of specimen]. When the bag and I started falling down a 10 m, 70 degree slope, I was more concerned about me."

GLEICHENIACEAE

Sticherus tepuiensis A. R. Smith, sp. nov. TYPE: Venezuela. Bolívar: Meseta del Jaua, Cerro Sarisariñama, porción nor-este, bosque enano por encima y al borde de la Sima Mayor, 4°41′40″N, 64°13′20″W, 1,320 m, 13 Feb. 1974, *Steyermark et al. 109036* (holotype, US). Figure 3E–J.

Ex affinitate *S. bifidi* (Willd.) Ching et specierum affinium, lamina adaxialiter in sicco brunneola vel rubro-brunnea nitenti, axibus infra furcas distales plerumque sine segmentis, sparsim squamatis, paleis gemmarum dormientium atrobrunneis vel atropurpureis, infirme ciliatis, paleis costarum rubro-brunneis, denticulatis, dentibus < 0.1 mm distinguendus.

Plants to 4 m or more long, sprawling; stipe brown or purple-brown toward the base, exceeding 3 mm diam., hard and brittle, glabrous; lamina with 2 or more pairs of opposite branches, the internode between them ca. 25 cm, primary branches forking again to give rise to secondary branches, each of these forking yet again to form deeply pinnatisect tertiary branches; each fork with a usually dormant bud at the base; dormant-bud scales dark brown to purplish brown, concolorous, lanceolate, ca. 2 × 0.2–0.3 mm, weakly ciliolate along the margin, cilia less than 0.1 mm; axes proximal to the penultimate segments tan to brownish, lacking indument or with very sparse small scales, commonly lacking segments, or sometimes with a few segments below the most distal forks; penultimate segments to ca. 40 cm × 2.5–3.2 cm; ultimate segments linear, perpendicular to the costa, ca. 2 mm wide at their base, separated by

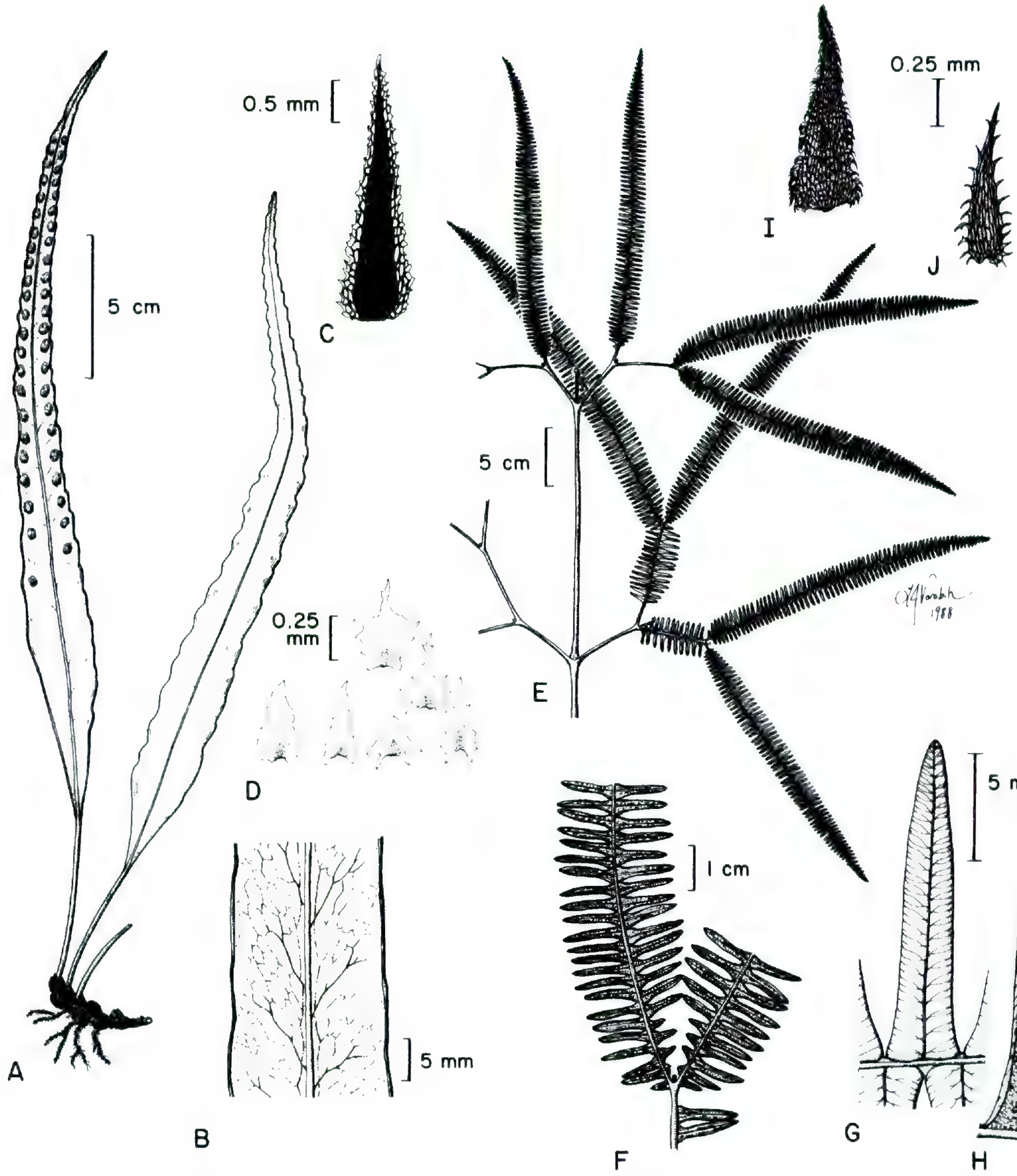

FIGURE 3. New species of *Sticherus* and *Pleopeltis*. A–D. *Pleopeltis repanda*, *Steyermark 88177*, UC.—A. Habit. —B. Portion of lamina, showing venation. —C. Scale from rhizome apex.—D. Microscales on abaxial lamina. E–J. *Sticherus tepuiensis*, *Steyermark et al. 109036*, US.—E. Habit, portion of lamina.—F. Portion of abaxial lamina at fork.—G. Segment, adaxial surface. H. Segment, abaxial surface. —I. Bud scale at fork.—J. Costal scale.

half to nearly their entire width, acute at the tip; costae reddish brown, bearing persistent, reddish brown, lanceolate scales to ca. 10 × 2 mm, these denticulate at their margin, teeth < 0.1 mm; laminar tissue glabrous adaxially, abaxially with tan, matted, crispate hairs nearly obscuring the lamina; veins 1-forked at or near their base, with up to ca. 25 pairs per segment; sporangia 3 or 4 per sorus.

Paratypes. VENEZUELA. BOLÍVAR: Meseta del Jaua, Cerro Sarisariñama, porción sur-oeste, entre la sabana y el salto arriba del campamento, al este del tributario del Río Marajano, 4°48′50″N, 64°34′10″W, 1,800 m, 26 Feb. 1974, *Steyermark et al. 109527* (US). TERRITORIO FEDERAL AMAZONAS: summit of Cerro Duida, on moist ridge top, 1,820–2,075m, 4 Sep. 1944, *Steyermark 58338* (US).

The lamina of this new species dries a rather shiny dark brown or reddish brown adaxially, as shown by all three collections seen. *Sticherus tepuiensis* has as its nearest allies members of the *S. bifidus* (Willd.) Ching alliance, which bear mat-

ted hairs on the lamina abaxially. A close relative may be *S. brevipubis* (Christ) A. R. Smith from southern Mexico and Central America. That species differs in having pectinate or sinuately winged axes proximal to the ultimate forks; bud scales with longer, whitish setae; and costal scales with longer setae often exceeding the width of the scale body.

Sticherus tomentosus (Cav. ex Sw.) A. R. Smith, comb. nov. *Mertensia tomentosa* Cav. ex Sw., Kongl. Vetensk. Acad. Nya Handl. 25: 177, t. 5, fig. 4. 1804. *Gleichenia tomentosa* (Cav. ex Sw.) Sprengel, Syst. Veg. 4: 27. 1827.

Sticherus velatus (Kunze) Copel., Gen. Filic. 28. 1947.

GRAMMITIDACEAE[2]

Ceradenia arthrothrix L. E. Bishop & A. R. Smith, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Atabapo, Cerro Marahuaca, above Salto Los Monos, on tributary of headwaters of Río Iguapo, 3°37′N, 65°23′W, 2,555 m, *Liesner 18008* (holotype, UC). Figure 4D–G.

Filicula parvula paleis rhizomatis minutis ciliis setuliformibus carentibus etiam lamina perpinnata setis conspicue septato-nodulosis instructa.

Rhizome very small, dorsiventral, with brown scales up to 0.6 × 0.3 mm, cordate at base, these (at least when young) with marginal glands but no setulose cilia; stipe black, 5–10 × 0.1–0.2 mm, set with scattered glandular hairs; rachis similar to stipe, terete, lacking setae; lamina probably pendent, perpinnate, up to at least 5 cm long, somewhat narrowed toward base, with prolonged apical growth (the complete apex not seen), soriferous from base or with a few basal pinnae sterile; pinnae suboblong or triangular-oblong, 3–5 × 1.5–2.0 mm, rather irregular due to the 2–4 pairs of sinuate lobes, set at 70–85° to the rachis, at base basiscopically constricted, straight, or shortly decurrent, acroscopically constricted or abruptly notched, at apex broadly rounded, at margin with scattered, conspicuously septate-nodulose, castaneous setae up to 0.7 mm long, otherwise glabrous, neither the costa nor the (always?) simple veins prominulous on either surface; stomata 38–45 × 36–42 μm; sori up to 3 pairs per segment, superficial, medial or slightly supramedial; sporangia 120–140 × 85–100 μm, with 13–15 annulus cells, the distal ones 18–21 μm high; spores globose or subglobose, 20–24 μm diam.

Paratype. Same locality as type, *Liesner 18009* (MO).

This remarkable little fern was noticed by Alan Smith associated with a specimen of *Selaginella*. It is apparently a reduced member of the *C. semiadnata* group. Like those species, it is perpinnate, and the lamina apex shows extended growth. The tendency of the setae on those species to be septate-nodulose is strongly developed in *C. arthrothrix*, and these setae constitute its most characteristic feature.

Ceradenia microcystis L. E. Bishop & A. R. Smith, sp. nov. TYPE: Venezuela. Bolívar: Dtto. Piar, Macizo del Chimantá, altiplanicie en la base meridional de los farallones superiores del Apacará-tepuí, sector Norte del Macizo, 5°20′N, 62°12′W, 2,200 m, *Steyermark, Huber & Carreño 128257* (holotype, UC; isotypes, MO, VEN not seen). Figure 5.

Est filix monticola quae in terra ad saxos perve occasionem in ramis viget, paleis rhizomatis castaneis cellulis medialibus insolenter parvis 25–35 μm latis et 2–4plo longioribus quam latioribus, pinnis setas marginales et aliquot pilos interspersos gerentibus.

Rhizome scales reddish brown, 2.5–4.0 × 0.3–0.7 mm, cordate or cordate-auriculate at base, fairly abrupt at tip, with marginal, hyaline or stramineous ciliae, the cells unusually small, medially 25–35-μm wide; stipe brownish black, nitid, near base with a few setae and many hyaline or brownish, branched hairs, 1.5–3 times as long as the lamina; rachis flexed basally, with sclerenchyma ± exposed on both sides, abaxially with scattered, short setae, adaxially with rather crowded, longer setae to 2 mm long; lamina deeply pinnatifid, narrowly oblong-triangular, usually broadest at base, with pinnae oblong, 2.5–3.5 mm wide, up to 25 mm long, fertile to the rounded apex, slightly dilated at base, at the entire or repand margin bearing antrorse setae intermixed with somewhat fewer and shorter branched hairs, on surface mostly glabrous and with the costa prominulous on either side; stomata 48–56 × 44–56 μm; each pinna with up to 10 pairs of sori, with capsules 195–220 × 140–160 μm, with annulus of 11–13 bow cells, these 28–32 μm high distally; spores hemispherical or subtetrahedral, 40–48 μm in longer diam.

[2] L. Earl Bishop, University Herbarium, University of California, Berkeley, California 94720, U.S.A., is principal author of the descriptions of three species in Grammitidaceae.

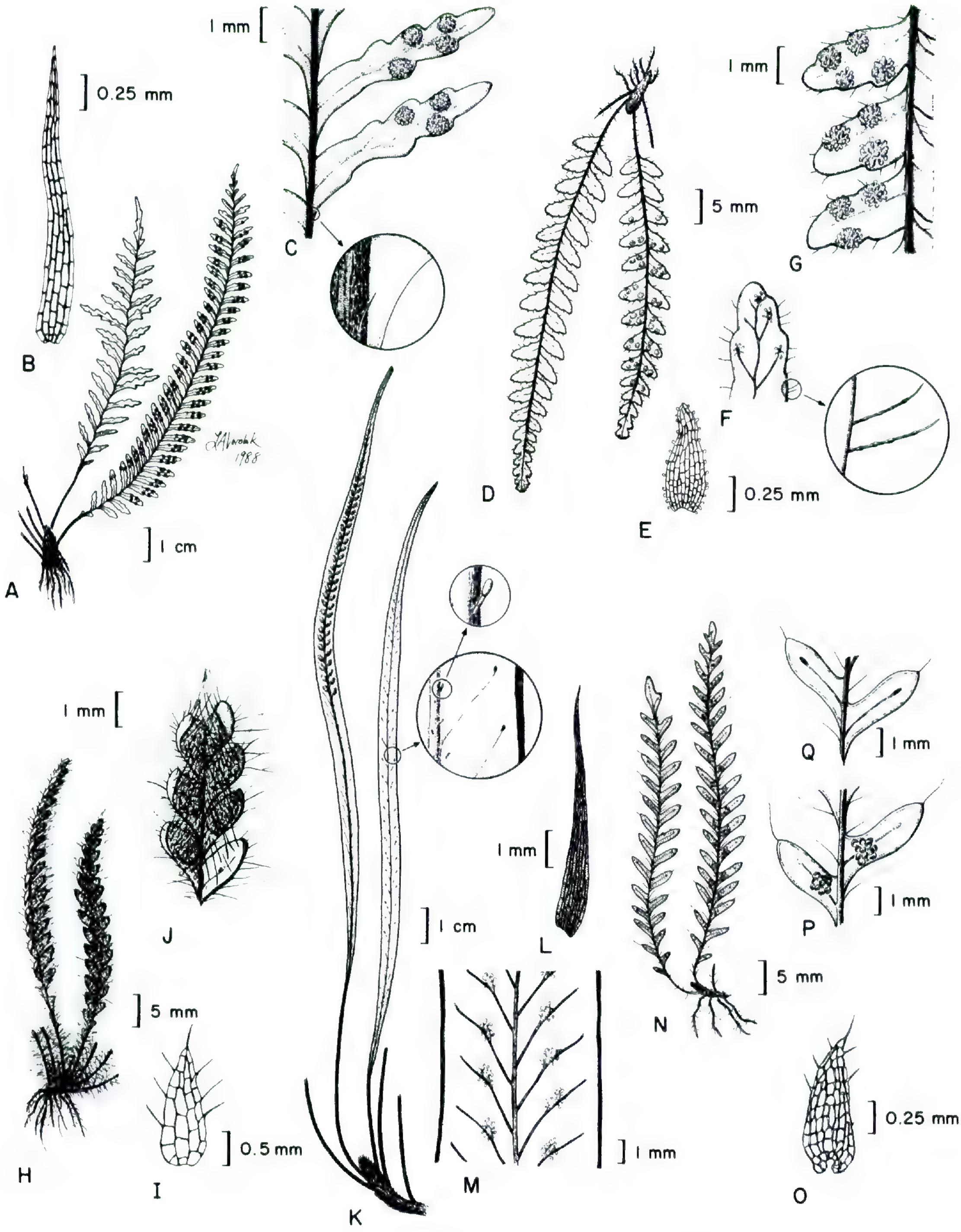

FIGURE 4. New species of Grammitidaceae. A–C. *Grammitis sinuosa*, *Maguire 24556*, NY.—A. Habit.—B. Scale from rhizome apex.—C. Pinnae, abaxial surface. D–G. *Ceradenia arthrothrix*, *Liesner 18008*, UC.—D. Habit.—E. Scale from rhizome apex.—F. Pinna apex and margin.—G. Pinnae, abaxial surface. H–J. *Grammitis plicata*.—H. Habit.—I. Scale from rhizome apex.—J. Pinnae, abaxial surface. K–L. *Grammitis peritimundi*, *Steyermark et al. 128719*, UC.—K. Habit, with details of indument.—L. Scale from rhizome apex.—M. Lamina, abaxial surface. N Q. *Grammitis liesneri*, *Liesner 18241*, UC.—N. Habit.—O. Scale from rhizome apex.—P. Pinnae, abaxial surface.—Q. Pinnae, adaxial surface.

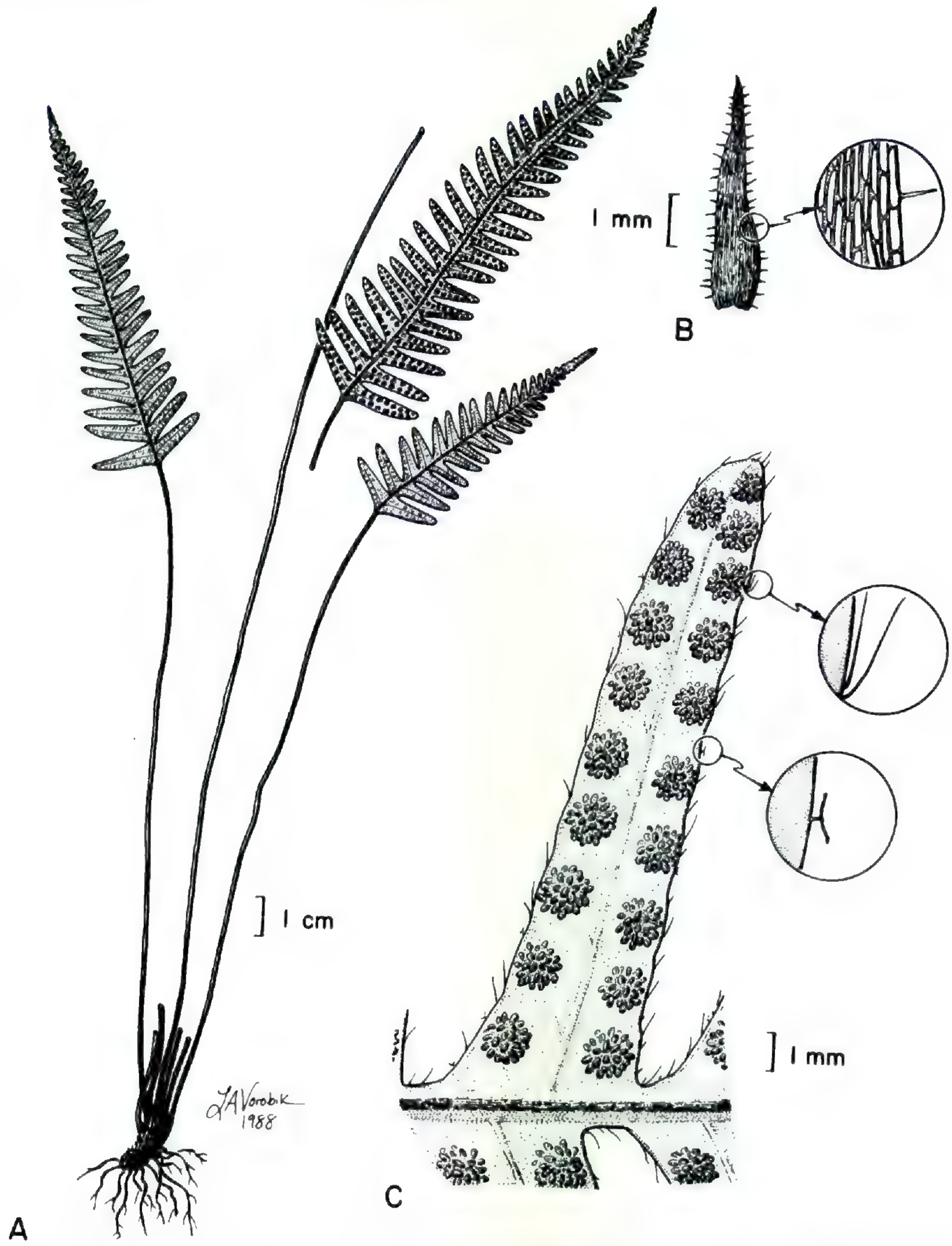

FIGURE 5. *Ceradenia microcystis, Steyermark et al. 128257*, UC. — A. Habit. — B. Rhizome scale, with detail. — C. Pinnae, abaxial surface, with details of marginal hairs.

The epithet refers to the unusually small cells of the rhizome scales.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dpto. Atures, 8 km NW of Yutaje, 5°41′N, 66°10′W, 1,500–1,760 m, *Liesner & Holst 21639A* (MO, UC). BOLÍVAR: Chimantá Massif, upper falls of Río Tirica, 1,950 m, *Steyermark & Wurdack 557* (F, NY, UC); Dtto. Piar, Macizo del Chimantá, Apacará-tepuí, ca. 2,200 m, *Steyermark et al. 128524* (UC, VEN not seen).

This species is most distinctive in the small cell size of its castaneous rhizome scales and the long-stiped fronds whose laminae bear setae and branched hairs on the margin. In the Guayana area, *C. spixiana*, mostly of lower elevations, is most similar and differs in its rhizome scales with larger cells and concolorous cilia, its lack of exposed sclerenchyma on either face of the central rachis, and the lack of branched hairs among the marginal laminar setae.

Grammitis blanchetii (C. Chr.) A. R. Smith, comb. nov. *Polypodium blanchetii* C. Chr., Bot. Tidsskr. 25: 78. 1902.

Polypodium nanum Fée, Gen. Filic. 238. 1852, not *Grammitis nana* Fée, 1853, nec Brackenr., 1854.

Grammitis liesneri A. R. Smith, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dpto. Atabapo, slope of Huachamacarí, 3°39′N, 65°43′W, 1,000–1,300 m, 5 Mar. 1985, *Liesner 18241* (holotype, UC). Figure 4N–Q.

Ex affinitate *G. taenifoliae* (Jenman) Proctor et specierum affinium pinnis uninervatis, linearibus, 4–5plo longioribus quam latioribus, lamina sparsim setosis, paleis rhizomatis aureis, setis marginalibus similiter coloratis distinguenda.

Plants on cliffs; rhizome ascending, up to 3.5 cm long, ca. 0.5–1 mm diam., at apex with ovate-lanceolate, stramineous to golden, nonclathrate, setose-margined scales 1–1.5 × 0.3–0.5 mm, scales decidedly cordate at base; fronds 3–5 cm long; stipe up to ca. 5 × 0.2 mm, atropurpureous, glabrous or with scattered dark reddish brown setae to 2 mm; lamina deeply pinnatisect to fully pinnate, proximal pinnae somewhat reduced; rachis reddish brown, glabrous or sparsely setose with dark reddish brown hairs to 2 mm; pinnae entire, linear, parallel-sided for most of their length, to ca. 5 × 1 mm, adnate and strongly decurrent at the base, ascending ca. 70–80° from rachis, with sinuses up to 2 mm wide; costae unbranched, glabrous or with an occasional single seta toward the base, ending adaxially in a clavate hydathode; laminar tissue glabrous on both sides, chartaceous; sori one per pinna, round, superficial, on the basal ¼ of costa near rachis, without paraphyses.

This species is a most distinct member belonging to the group of *G. taenifolia* (Jenman) Proctor and *G. blanchetii* but differs from those and other similar species in the one-nerved pinnae, linear segments 4–5 times longer than wide, and golden rhizome scales with similarly colored marginal setae (setae and often scale margins darkened in the two allied species). *Grammitis liesneri* is less hairy than most of its closest relatives. It is named for its collector, who has made numerous important collections of pteridophytes from the Guayana.

Grammitis peritimundi L. E. Bishop & A. R. Smith, sp. nov. TYPE: Venezuela. Bolívar: Dtto. Piar, Macizo del Chimantá, pequeñas altiplanicies en la base septentrional de los farallones superiores del Amurí-tepuí, 5°10′N, 62°07′W, 1,950 m, *Steyermark, Huber & Carreño 128719* (holotype, UC; isotypes, MO, VEN not seen). Figure 4K–L.

Grammitis major epiphytica vel lithophytica quae in Scuto Guayano endemica est, paleis rhizomatis brunneis, lamina plerumque lineari-elliptica usque ad 26 cm longa, hydathodis laminae adaxilaris distincte et regulatim evidentibus.

Rhizome scales medium brown, up to 4 × 0.6 mm, cordate-auriculate, entire, medial cells 40–80 × 15–30 μm; stipe brown or blackish brown, glabrous, 0.3–0.6 mm wide at very base, soon alate distally; costa prominulous on either side, at times with the sclerenchyma exposed abaxially; veins well sclerenchymatized, somewhat prominulous on either side, ascending 35–50° to the costa, the sterile ones simple, adaxially with distinct hydathodes regularly developed at their distal ends; lamina 3–7 mm wide, fertile from the middle, occasionally to the tip but more often with a prolonged, acuminate, sterile apex; marginal sclerenchyma substriolate, 1.0–1.5 mm wide; hairs on margin when young usually branched, at maturity usually lost, those on midrib mostly simple, catenate or brown, 3–5-celled with terminal cell often enlarged; stomata 52–62 × 50–55 μm; sori extending from near costa to less than halfway to margin; capsules broadly obpyriform, 80–90 × 72–80 μm, with 9–11 annulus cells, the distal ones 30–38 μm high; spores minutely papillate, subglobose, 22–26 μm diam.

Paratypes. VENEZUELA. BOLÍVAR: Dtto. Piar, Murisipan-tepuí, summit, lithophyte in deep shaded crevice, 2,300 m, *Holst 3531* (UC); Mt. Roraima summit, 8,600 ft., *McConnell & Quelch 568* (US); *Mt. Roraima Expedition 307* (US); Chimantá Massif, Torono-tepuí, in wet soil in waterfall spray, 1,880–1,970 m, *Steyermark & Wurdack 1176* (US); Cerro Jaua, epiphyte on slender tree along stream, 1,922–2,100 m, *Steyermark 98005* (US); Ptari-tepuí, crevices of zanjon, 2,360–2,420 m, *Steyermark et al. 115689* (UC); Macizo del Chimantá, Apacará-tepuí, crevices of bluff, 2,200 m, *Steyermark et al. 128534* (UC); Macizo del Chimantá, Amurí-tepuí, epiphyte in low forest along stream, 1,850 m, *Steyermark et al. 128631* (MO, UC); Auyan-tepuí, 1,850 m, *Vareschi & Foldats 4817* (US); Auyan-tepuí, 2,300 m, *Vareschi & Foldats 4928* (US). TERRITORIO FEDERAL AMAZONAS: Cerro de la Neblina, epiphyte, 1,950 m, *Boom et al. 6007* (UC); Cerro de la Neblina, epiphyte, 1,750–1,850 m, *Liesner 16080* (UC); Atabapo, Huachamacarí, epiphyte, 1,720 m, *Liesner 18133* (UC); Cerro de la Neblina, epiphyte on mossy tree trunk, 2,200 m, *Plowman & Thomas 13635* (UC); Atabapo, Cerro Marahuaca, rock crevices, 2,520–2,650 m, *Steyermark & Holst 130812* (UC); Atabapo, Cerro Marahuaca, epiphyte, 1,560 m, *Steyermark 129618* (UC).

This large species is most similar to *G. fluminensis*, with which it shares large lamina size, large stomata, and linear-elliptic fronds. It differs in the regular, clear development of the adaxial hydathodes. In addition to having hydathodes, *G. peritimundi* differs from the sympatric *G. bryophila* in its medium brown (vs. golden brown) scales.

The epithet is derived from *peritus* (lost) and *mundus* (world), in reference to a fantasy by H. G. Wells set on Mt. Roraima.

Grammitis plicata A. R. Smith, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Serranía Parú, Caño Asísa, Río Ventuari, cumbre

just S of valley head of Camp Stream, 2,000 m, 2 Feb. 1951, *Cowan & Wurdack 31164* (holotype, UC; isotype, NY). Figure 4H–J.

G. blanchetii (C. Chr.) A. R. Smith affinis, a qua imprimis differt pinnis uninervatis, lamina densius setosa subcoriacea plicata conduplicata.

Plants epiphytic; rhizome suberect, ca. 1 mm diam., at apex with lanceolate, golden brown, non-clathrate scales ca. 1–1.5 × 0.2–0.3 mm, scales setose along margin, especially toward apex, setae dark reddish brown; fronds mostly 3–5 cm, tightly clustered; stipe ca. 5 × 0.2 mm, with numerous dark red-brown setae to 3 mm; lamina often conduplicately folded, pinnatisect nearly or quite to rachis, with gradually reduced and more distant proximal segments; rachis brownish to blackish, with numerous setae to 3 mm on both sides; pinnae oblong, 1.5–2 × 1 mm, strongly adnate and decurrent, not gibbous, cut to rachis but with bases contiguous, ascending ca. 60° from rachis, separated by less than 0.5 mm distally to more than 1 mm proximally; lamina tissue subcoriaceous, with stiff setae on both sides; veins simple and unbranched, ending in obscure hydathodes adaxially; sorus one per pinna, occupying the basal half of a vein, confluent with sori of adjacent pinnae and across the rachis, intermixed with stiff setae.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dpto. Río Negro, Cerro Aracamuni, summit, Popa Camp, 1°26′N, 65°47′W, 1,550 m, *Liesner & Delascio 21999* (UC); Dpto. Río Negro, Cerro Aracamuni, summit, Proa Camp, 1°32′N, 65°49′W, 1,400 m, 30 Oct. 1987, *Liesner & Carnevali 22662* (UC); Dpto. Atures, valley of Río Coro-Coro, W of Serranía de Yutaje, E base of forested mountain 5 km W of river, 5°41′N, 66°09′30″W, 1,100 m, 13 Mar. 1987, *Holst & Liesner 3456* (MO, UC); Dpto. Atabapo, slope of Cerro de Marahuaca, Río Yameduaka arriba, 3°38′N, 65°28′W, 1,225 m, 19 Feb. 1985, *Liesner 17674* (UC). BOLÍVAR: Cerro Marutani, Dtto. Heres, 3° 50′N, 62°15′W, 1,200 m, 11–14 Jan. 1981, *Steyermark et al. 123952* (MO).

This species seems most closely related to *G. blanchetii* but differs by having one-nerved pinnae, more densely and longer-setose lamina, and subcoriaceous, usually conduplicately folded lamina. *Grammitis plicata* grows at higher elevations than *G. blanchetii*, which is typically a lowland species.

Grammitis sinuosa A. R. Smith, sp. nov. TYPE: Surinam: Tafelberg, 29 Aug. 1944, *Maguire 24556* (holotype, NY). Figure 4A–C.

Ex affinitate *G. suspensae* (L.) Proctor et specierum affinium margine pinnarum sinuato, soris superficialibus nec profunde immersis nec restrictis ad apicem pinnarum, lamina latiore et breviore, textura chartacea distinguenda.

Plants epiphytic; rhizome suberect, ca. 1 mm diam., at apex with lanceolate, brown, clathrate, glabrous, entire scales ca. 2–3 × 0.2–0.3 mm; fronds tightly clustered, 8–12 cm long; stipe 0.2–0.3 mm diam., faintly winged, glabrous; lamina deeply pinnatisect to barely pinnate, with gradually reduced proximal pinnae, ultimately reduced to a narrow, sinuate wing extending to the rhizome, distally reduced gradually to a pinnatifid apex; rachis atropurpureous to dark reddish brown, glabrous or with a few tan hairs 0.1–0.3 mm; pinnae sinuately lobed or pinnatifid, mostly 8–15 × 2–3 mm, strongly adnate and decurrent, rounded at the tip, cut to the rachis but with bases contiguous, ascending ca. 60° from rachis, separated their width or sometimes slightly more; costae 3–5 mm apart, brownish, sinuous, glabrous; laminar tissue glabrous on both sides; veins 3–5 pairs per segment, ending well before the margin in clavate hydathodes adaxially; sori 2–4 pairs per pinna, round or slightly oblong, slightly sunken or superficial, without paraphyses.

Paratypes. GUYANA: Essequibo River, 1899, *Jenman s.n.* (NY). VENEZUELA. BOLÍVAR: Dtto. Piar, summit of Amaruay-tepuí, S side of E half, 5°55′N, 62°13′W, 950–1,100 m, 11 May 1986, *Liesner & Holst 20812* (MO, UC). TERRITORIO FEDERAL AMAZONAS: Cerro Sipapo (Paráque), breaks below Lower Camp Savanna, 15 Dec. 1948, *Maguire & Politi 27710* (UC); Dpto. Atabapo, near base of Duida, 3°34′N, 65°32′W, 1,000 m, 25 Oct. 1988, *Liesner 25394* (UC); Dpto. Atabapo, Cerro Huachamacarí, E slope, 3°49′N, 65°42′W, 600–700 m, 3 Nov. 1988, *Liesner 25778* (UC).

This species may be related to *G. suspensa* (L.) Proctor, but the latter differs in having entire pinnae, sori more deeply sunken in pits and tending to be localized at the pinna tips, thicker texture, and longer, narrower laminae. At a higher level, *G. sinuosa* is a member of the group with entire, clathrate rhizome scales comprising such species as *G. moniliformis* (Lag. ex Sw.) Proctor, *G. firma* (J. Smith) C. Morton, and many others.

POLYPODIACEAE

Pleopeltis repanda A. R. Smith, sp.nov. TYPE: Venezuela. Bolívar: Altiplanicie de Nuria, E of Miamo, upper part of W-facing wooded slopes, 8 Jan. 1961, *Steyermark 88177* (holotype, UC). Figure 3A–D.

Differt a *P. macrocarpa* (Bory ex Willd.) Kaulf. lamina abaxialiter glabra vel sparsim squamata, soris paraphysibus et squamis carentibus, margine laminae undulato vel repando.

Plants epiphytic; rhizome creeping, ca. 3 mm diam., bearing dense, lanceolate scales ca. 2–3 ×

0.3 mm with a broad, blackish central stripe and narrow, tan, erose-denticulate margins; fronds to 30 cm long, undivided; stipe up to ca. 5 cm × 2 mm, brownish, ± glabrous; lamina coriaceous, narrowly elliptic but broadest in the basal ¼, cuneate at the base, 1.7–2.8 cm wide, acute at the tip, with a sinuate or repand margin, especially in fertile portion of lamina, crenations slightly broader than the sorus length, 1–2 mm deep; rachis stramineous to tan, glabrous or with a few minute scales to 5 mm long; laminar tissue glabrous on both sides, or abaxially with a very few minute, tan to brownish, ovate-attenuate scales to ca. 0.5 × 0.1–0.2 mm; sori confined to the distal ⅓–⅔ of the lamina, in a single supramedial to submarginal row on each side of the rachis, nonindusiate, oblong, to 5 × 3 mm, lacking scales and paraphyses, even when young.

Paratype. VENEZUELA. BOLÍVAR: Río Samay, *Holst & Liesner 2434* (MO).

This species differs from all other simple-bladed *Pleopeltis* species in the Neotropics by the abaxially nearly scaleless lamina and by the lack of scales or paraphyses in the sori. It also has a more undulate or sinuate margin than its closest relatives, e.g., *P. macrocarpa* (Bory ex Willd.) Kaulf.

PTERIDACEAE

Adiantum amazonicum A. R. Smith, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dpto. Atabapo, SE bank of middle part of Caño Yagua at Cucurital de Yagua, 03°36′N, 66°34′W, ca. 120 m, 8 May 1979, evergreen forest with *Leopoldinia* palms very dominant, *Davidse, Huber & Tillett 17429* (holotype, UC; isotypes, MO, VEN not seen). Figure 6C–E.

A. cajennensi Klotzsch et *A. Tetraphyllo* Humb. & Bonpl. ex Willd. maxime simile, sed pinnulis integris, ad apicem rotundatis, indusiis rufopilosis, squamis rhachidis valde dentatis aut setosis.

Rhizome short-creeping, ca. 3–4 mm diam., with internodes 2–3 mm apart; rhizome scales dark brown or blackish with lighter margins, denticulate on the margin, 1–1.5 × 0.2–0.3 mm; fronds to ca. 65 cm long; stipe to ca. 40 cm × 1–2 mm, dark reddish brown to atropurpureous, shining, glabrescent; rachis similarly colored and with numerous reddish brown hairs and linear-lanceolate, setose-margined scales to ca. 2 × 0.1 mm; lamina 2-pinnate, with 2–5 pairs of lateral pinnae and a similar terminal one; pinnae 1-pinnate, the pinnules sessile or stalked less than 1 mm at the pinna base, oblong, dimidiate, sterile margins entire or crenulate, rounded at the tip, straight; laminar tissue abaxially with scattered reddish brown scales with an expanded, stellate base; veins forking, free; sori in oblong patches along acroscopic margin and tip of pinnule, mostly 8–12 per pinnule; indusium adaxially with reddish brown hairs.

Paratypes. BRAZIL. RONDÔNIA: track from Mutumparaná to Rio Madeira, 30 Nov. 1963, *Prance et al. 9012A* (NY not seen, UC); km 90 93, Madeira-Mamoré railroad, near Jaciparaná, 30 June 1968, *Prance et al. 5399* (NY not seen, UC).

This is most similar to *A. cajennense* Klotzsch, *A. fuliginosum* Fée, and *A. tetraphyllum* Humb. & Bonpl. ex Willd. From all three it differs in having oblong, more or less entire pinnules with rounded tips and indusia with reddish brown hairs adaxially. From *A. fuliginosum*, *A. amazonicum* also differs in the less densely scaly rachis but it agrees in having the rachis scales toothed or setose. This contrasts with the condition in *A. cajennense* and *A. tetraphyllum*, which have nearly entire, linear or hairlike rachis scales.

Adiantum nudum A. R. Smith, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dpto. Río Negro, E of Cerro de La Neblina Base Camp, along Río Mawarinuma, 0°50′N, 66°09′W, 140 m, 2 May 1984, along stream banks, *Thomas 3326* (holotype, UC; isotypes, MO, NY not seen). Figure 6A–B.

Differt a *A. petiolato* statura minore stipitibus gracilioribus, stipite et rhachidi glabra, rhizomate breviter repenti internodiis brevissimis, pinnis paucioribus plerumque 1–4-jugatis, petiolulis pinnarum glabris.

Rhizome long-creeping, 1.5–2 mm diam., with internodes ca. 1–2 mm apart; rhizome scales castaneous, shining, entire, ca. 1.5 × 0.1–0.15 mm; fronds 8–25 cm long; stipe 3–12 cm × 0.4–0.8 mm, atropurpureous to blackish, shining, glabrous; rachis similarly colored, also glabrous; lamina 1-pinnate, with 1–4 lateral pinna pairs and a triangular terminal segment; pinnae oblong, short-stalked 1–3 mm, 1.5–3.5 × (0.5–)1–1.6 cm, obtuse at tip, sterile margins evenly serrulate, at the base inequilateral with the basiscopic side excavate, acroscopic side rounded, pinnae becoming equilateral toward the tip; laminar tissue glabrous on both sides; veins forking, free; sori in oblong to linear patches along acroscopic margin, tip, and most of basiscopic margin except for excised basal portion.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dpto. Río Negro, 1.5 km E of Cerro de la

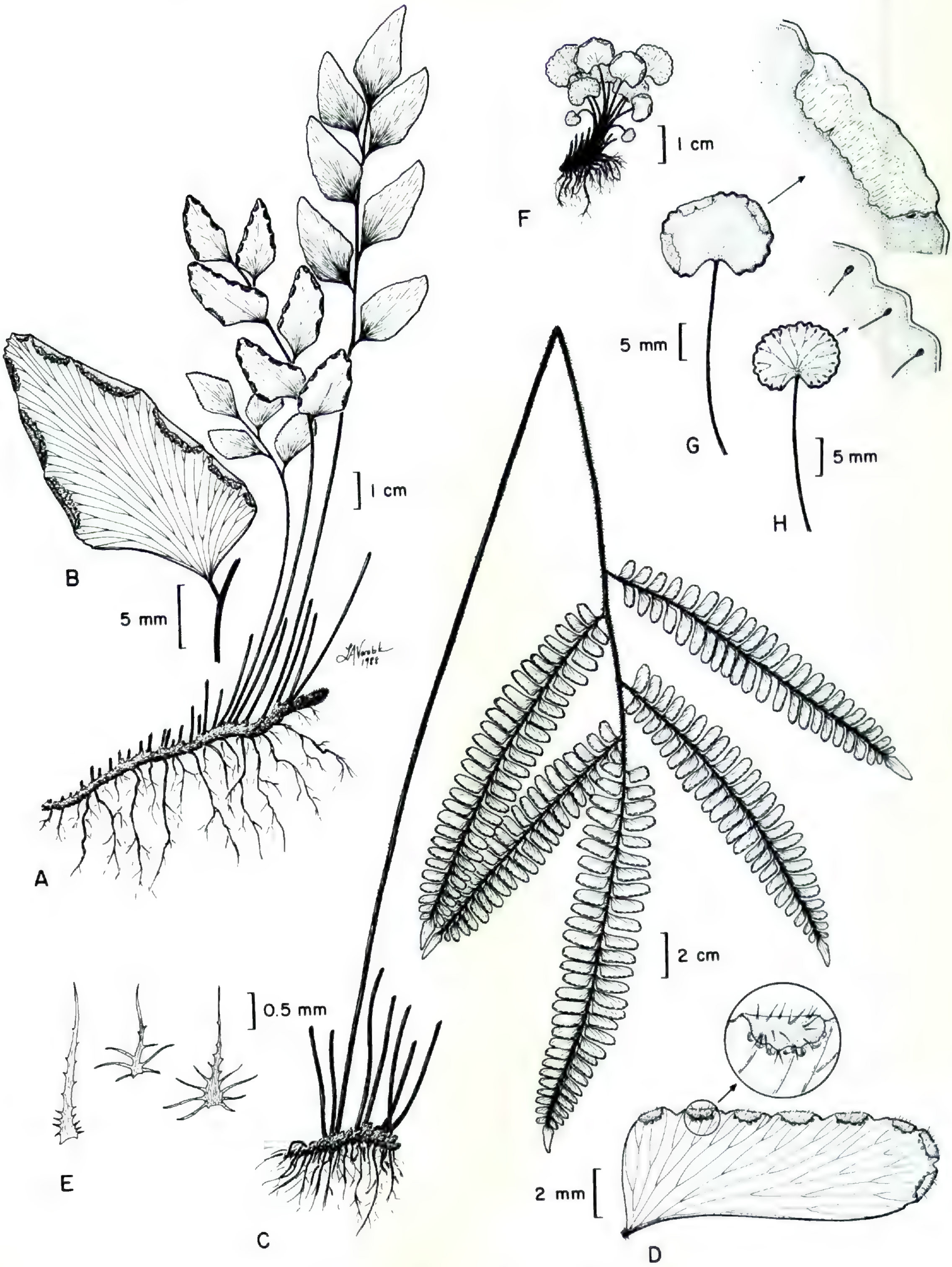

FIGURE 6. New species of Pteridaceae. A–B. *Adiantum nudum*, *Thomas 3326*, UC.—A. Habit.—B. Pinnae, abaxial surface. C–E. *Adiantum amazonicum*, *Davidse et al. 17429*, UC.—C. Habit.—D. Pinnule, with detail of sorus, abaxial surface.—E. Scales from rachis. F–H. *Doryopteris cyclophylla*, *Davidse & Miller 27341*, UC.—F. Habit.—G. Frond, with detail of sorus, abaxial surface.—H. Frond, with detail of margin to show hydathodes, adaxial surface.

Neblina Base Camp on the Río Mawarinuma, 0–3 km S of main river, 140 m, 2–3 Dec. 1984, stream bank, *Liesner 17407* (MO, UC), *Liesner 17416* (MO). BARINAS: along Río Caparo, 2–4 km up river from dam side, 07°41′N, 71°28′W, ca. 100–200 m, 12 Mar. 1980, *Liesner & González 9452* (MO not seen, UC). BRAZIL. MATO GROSSO: 20 km S of Xavatina, 400 m, 15 June 1966, *Irwin et al. 17092* (MO).

This appears to be most closely related to *A. petiolatum* Desv. but differs by the completely glabrous stipe, rachis, and pinna stalks; rhizome with very short internodes (vs. internodes often more than 1 cm in *A. petiolatum*); smaller stature of the plants with thinner stipes; fewer pinna pairs (mostly 5–10 in *A. petiolatum*); and longer pinna stalks.

Doryopteris cyclophylla A. R. Smith, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dpto. Río Negro, Neblina Massif, Canyon Grande, along Río Mawarinuma between the mouth of canyon and first major fork of river, ca. 7 airline km ENE of Puerto Chimo, 0°50–51′N, 66°02–06′W, 400–700 m, on cliff, in cracks, in trickle of water, 9–14 July 1984, *Davidse & Miller 27341* (holotype, UC; isotype, MO not seen). Figure 6F–H.

Species frondibus minimis rotundatis vel subcordatis, laminis membranaceis a congeneribus diversa.

Rhizome compact, suberect, caudex ca. 5–8 mm diam.; rhizome scales tan, concolorous, entire, ca. 1 × 0.2 mm; fronds monomorphic, 1–3 cm long, densely tufted; stipe to ca. 25 × 0.2–0.3 mm, terete, atropurpureous to blackish, shining, glabrous, widened at the point of attachment to the lamina; lamina subrotund to subcordate, up to 10 × 13 mm, usually a little broader than long, entire or faintly crenulate on the margin, lacking buds at the base; laminar tissue glabrous, thin; veins forking, free, ending short of the margin in distinct, clavate hydathodes adaxially; sori in elongate patches or subcontinuous at the margin, the indusium scarious and ca. 1 mm wide, strongly reflexed.

This is readily distinguishable from all other *Doryopteris* species by the very small frond with its round or subcordate rather thin lamina.

Doryopteris davidsei A. R. Smith, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dpto. Atures, 23 km NE of Puerto Ayacucho and 10 km E of hwy., hills and base of hills near Cachama, 5°51′N, 67°24′W, 90 m, 17–19 Apr. 1978, on large, mossy boulders, *Davidse & Huber 15315* (holotype, MO).

Frondes 5–10 cm longae; paleae rhizomatis bicolores; stipes adaxialiter complanatus, pilis minutis 0.1 mm longis praeditus; lamina profunde cordata, 3 × 1.8 cm, ad apicem acuta; venae areolatae, terminantes adaxialiter in hydathodos.

Rhizome compact, suberect, caudex 5–8 mm diam.; rhizome scales bicolorous, with a castaneous central stripe and narrower, tan margins, entire, ca. 2.0–2.5 × 0.2 mm; fronds monomorphic, 5–10 cm long, clustered; stipe ca. 4–7 × 0.3–0.4 mm, dark brown to atropurpureous, shining, adaxially flattened and bearing numerous glandular castaneous hairs 0.1 mm long on the flattened portion; laminae narrowly and deeply cordate, up to 3 × 1.8 cm, nearly twice as long as broad, basal lobes rounded, acute or acuminate at the tip, crenulate along the sterile margin, lacking buds at the base; laminar tissue glabrous, thin; veins forming elongate polygonal (often hexagonal) areoles in 2–4 series, the ultimate veins ending short of the margin in distinct, clavate hydathodes adaxially; sori continuous along the basal and outer margins but with distal ⅓ of lamina sterile, the indusium scarious and ca. 0.4 mm wide.

The affinities of this species are uncertain. Because of the simple, deeply cordate blades, it will key to near *D. sagittifolia* (Raddi) J. Smith, but *D. davidsei* has much smaller fronds, round rather than acute basal lobes, and thin texture. The small, thin fronds suggest relationship with *D. cyclophylla*, but that species differs in having free veins; lamina as broad as or broader than long; tan, concolorous rhizome scales; and a wider indusium.

SELAGINELLACEAE

Selaginella albolineata A. R. Smith, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dpto. Atures, Río Coro-Coro, W of Serranía de Yutaje, 6–8 km N of settlement of Yutaje, 05°41′N, 66°07′30″W, 320 m, 23 Feb. 1987, *Liesner & Holst 21341* (holotype, UC; isotype, MO). Figure 7A–E.

Caules repentes, 0.2–0.3 mm diam., non articulati, apicibus flagelliformibus et sobolibus carentes, rhizophoris filiformibus 0.1 mm diam. per totam longitudinem caulis; folia ubique dimorpha, membranacea, utrinque glabra, striis albidis vel translucentibus longitudinalibus; folia intermedia ovata, usque ad 1.0 × 0.7 mm, acuminata, margine denticulata et obscure albida; folia laterales usque ad 1.8 × 1.2 mm, ad apicem rotundata, integra; sporophylla pauca lanceolata plerumque patentia laxe aggregata.

Plants on moist rocks, ca. 5 cm long, branch system anisotomous and ca. 3 times divided, branches arising along length of main stem; main

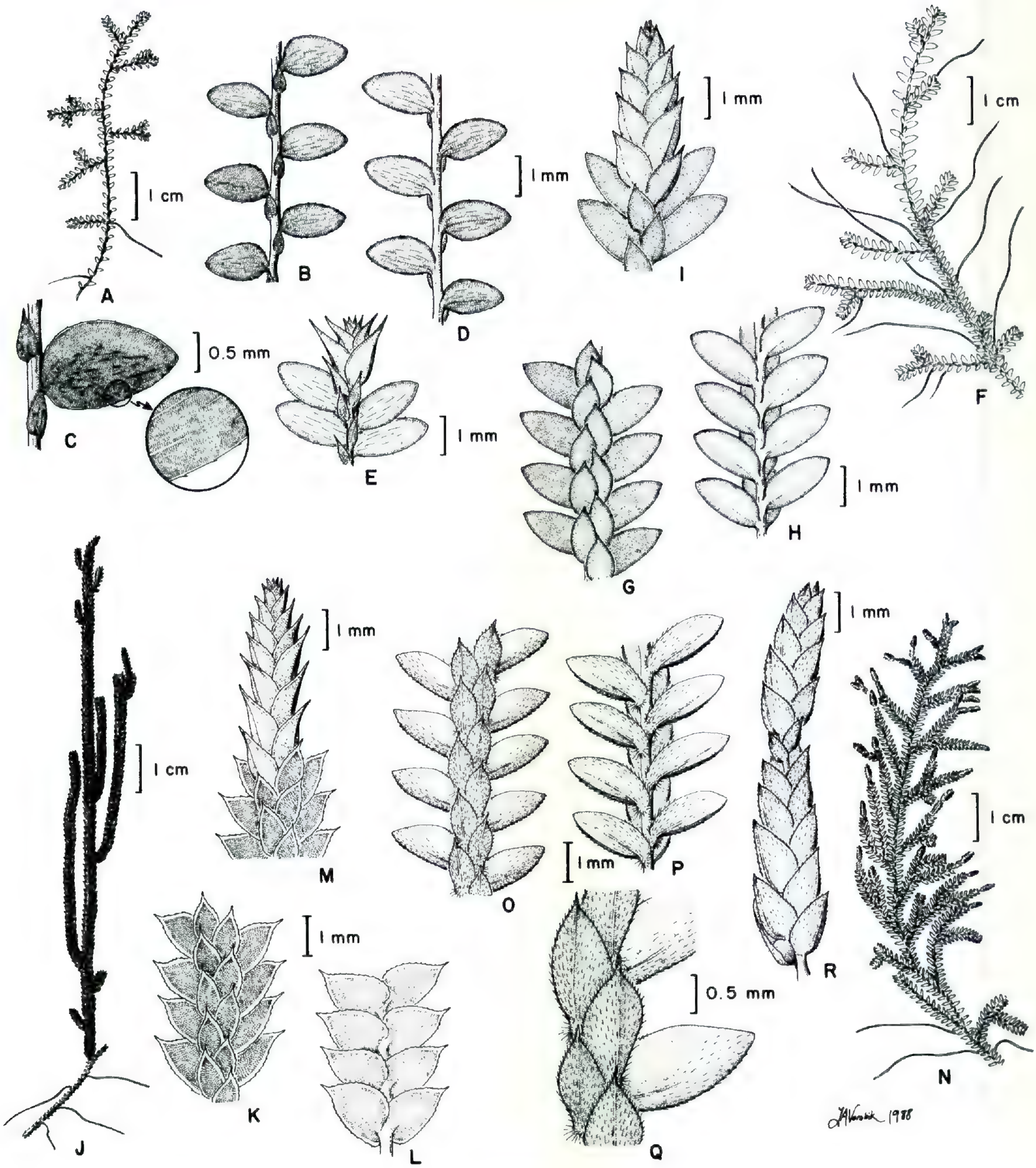

FIGURE 7. New species of *Selaginella*. A–E. *Selaginella albolineata, Liesner & Holst 21341*, UC.—A. Habit.—B. Adaxial surface.—C. Lateral leaf, with detail.—D. Abaxial surface.—E. Fertile portion. F–I. *Selaginella marahuacae, Liesner 18008*, UC.—F. Habit.—G. Adaxial surface.—H. Abaxial surface.—I. Fertile portion. J–M. *Selaginella arrecta, Holst & Liesner 3332*, UC.—J. Habit.—K. Adaxial surface.—L. Abaxial surface.—M. Fertile portion. N–R. *Selaginella pubens, Maguire & Politi 27634*, UC.—N. Habit.—O. Adaxial surface.—P. Abaxial surface.—Q. Adaxial surface, detail.—R. Fertile portion.

stems 0.2–0.3 mm diam., creeping, nonarticulate, bearing filiform rhizophores 0.1 mm diam. along their length; leaves dimorphous throughout, light green, dull, thin-textured; medial leaves ovate, to ca. 1.0 × 0.7 mm, acuminate at apex, truncate at base, denticulate from a very narrow and not very prominent whitish margin, with numerous, narrow, whitish or translucent, longitudinal streaks; lateral leaves to 1.8 × 1.2 mm, rounded at tip and base, inequilateral, planar, entire or nearly so, also with streaks like those of medial leaves; strobili consisting of only a few sporophylls, not tetrago-

nous; sporophylls lanceolate, ± spreading, loosely aggregated; megaspores ca. 150 μm diam., light yellowish, ± smooth; microspores not seen.

This is perhaps related to *S. potaroensis* Jenman or some similar species, but *S. potaroensis* differs in having acute and larger lateral leaves that are often minutely pubescent on the basiscopic side adaxially and in having median leaves less than half the length of the lateral leaves. Another close relative may be *S. porelloides* (Lam.) Spring, which has thicker stems and larger, firmer leaves. Both of these possible relatives lack the streaking in the leaves that is characteristic of *S. albolineata*. Such streaking has been seen to a lesser extent in other species of *Selaginella*. The systematic significance of this character is unknown.

Selaginella arrecta A. R. Smith, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dpto. Atures, valley of Río Coro-Coro, W of Serranía de Yutaje, 05°42′N, 66°09′30″W, 1,250 m, 6 Mar. 1987, *Holst & Liesner 3332* (holotype, UC; isotype, MO not seen). Figure 7J–M.

S. vernicosae affinis, a qua imprimis differt marginibus foliorum intermediorum et lateralium late albidis ca. 6 cellulis latis, foliis intermediis denticulatis ad apicem aristatis, foliis lateralibus acutis vel breviaristatis.

Plants on moist banks and on mossy rocks in or adjacent to streams, to ca. 20 cm; main stems ca. 0.5 mm diam., erect, width with leaves 2–3 mm, sparingly branched, branches simple, strongly ascending, nearly parallel to main stem, nonarticulate, bearing only a few, short, filiform rhizophores 0.2 mm diam. at the very base of main stem; leaves dimorphous throughout, dark olive-green above, yellow-green below, firm and subcoriaceous; medial leaves ovate, to 1.8 × 1 mm, short-aristate at apex, truncate at the hidden base, strongly overlapping, denticulate from a broad whitish margin ca. 6 cells wide; lateral leaves broadly ovate, to 1.8 × 1.5 mm, strongly overlapping, acute to short-aristate at the apex, denticulate from a broad, whitish margin; strobili tetragonous, to ca. 10 × 1.5–2 mm at tips of lateral branches; sporophylls ovate-lanceolate, to 2 mm long; megaspores not basal, ca. 200–300 μm diam., light yellowish, with faintly raised ridges; microspores shed singly, orange.

Paratypes. VENEZUELA. BOLÍVAR: cumbre del Cerro Guaiquinima, sector suroeste-central, a lo largo del afluente suroccidental del Río Carapo, 05°45′N, 63°35′W, 950 m, 26 May 1978, *Steyermark et al. 117478* (MO, UC). TERRITORIO FEDERAL AMAZONAS: Serranía Yutaje, Río Manapiare, Cerro Yutaje, along left fork of Caño Yutaje, 1,250 m, 12 Feb. 1953, *Maguire & Maguire 35204* (UC); Cerro Sipapo (Paráque), lower Caño Negro, 1,400 m, 25 Dec. 1948, *Maguire & Politi 27920* (UC).

This is most closely related to *S. vernicosa* Baker, which differs in lacking broad whitish margins on the nonaristate median and lateral leaves and in having shortly and finely ciliate median leaves.

Selaginella beitelii A. R. Smith, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Cerro de la Neblina, Camp 7, 5.1 km NE Pico Phelps, along Caño Gardner, 0°50′40″N, 65°58′10″W, 1,735 m, 30 Jan. 1985, *Beitel 85079* (holotype, UC; isotype, NY not seen). Figure 8I–L.

Caules ca. 0.7 mm diam., non articulati, apicibus flagelliformibus et sobolibus carentes, rhizophoris filiformibus 0.1 mm diam. per totam longitudinem caulis praediti; folia ubique dimorpha, chartacea, veneta adaxialiter in statu vivo, utrinque glabra; folia intermedia late ovata, integra, ca. 1.5–2.5 × 1.2–1.8 mm, ad apicem acuta, non aristata, ad marginem obscure albida vel margine virello; folia laterales late ovata, 3.0–4.0 × 1.6–2.5 mm, basi inaequaliter rotundata, ad marginem acroscopicum denticulata, ad apicem rotundata vel subacuta; strobili tetragoni; sporophylla ovato-lanceolata, margine denticulata.

Plants terrestrial or epiphytic, branch system anisotomous and 2 or 3 times divided, branches arising perpendicularly all along main stems; stems to ca. 0.7 mm diam., prostrate, lacking flagelliform tips or sobols, nonarticulate, bearing filiform rhizophores 0.1 mm diam. along their length; leaves dimorphous throughout, bluish green adaxially when living, silvery green abaxially, chartaceous, glabrous on both surfaces; medial leaves broadly ovate, with a very narrow and inconspicuous whitish border, or whitish border lacking, ca. 1.5–2.5 × 1.2–1.8 mm, truncate at base, acute at apex, lacking an aristate tip; lateral leaves broadly ovate, 3.0–4.0 × 1.6–2.5 mm, unequally rounded at base with acroscopic portion strongly overlapping stem, denticulate along acroscopic margin, rounded or subacute at apex; strobili tetragonous; sporophylls ovate-lanceolate, to ca. 1.5 mm long, denticulate along margin.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro de la Neblina, Camp 12, 1,950 m, *Boom et al. 6012* (NY not seen, UC).

This seems most similar to *S. muscosa* Spring in C. Martius but differs in the acute, nonaristate median leaves and bluish green color. It is also similar to *S. rhodostachya*, from which it differs in its broader branches, ca. 5 mm wide, and more overlapping lateral leaves, especially toward the

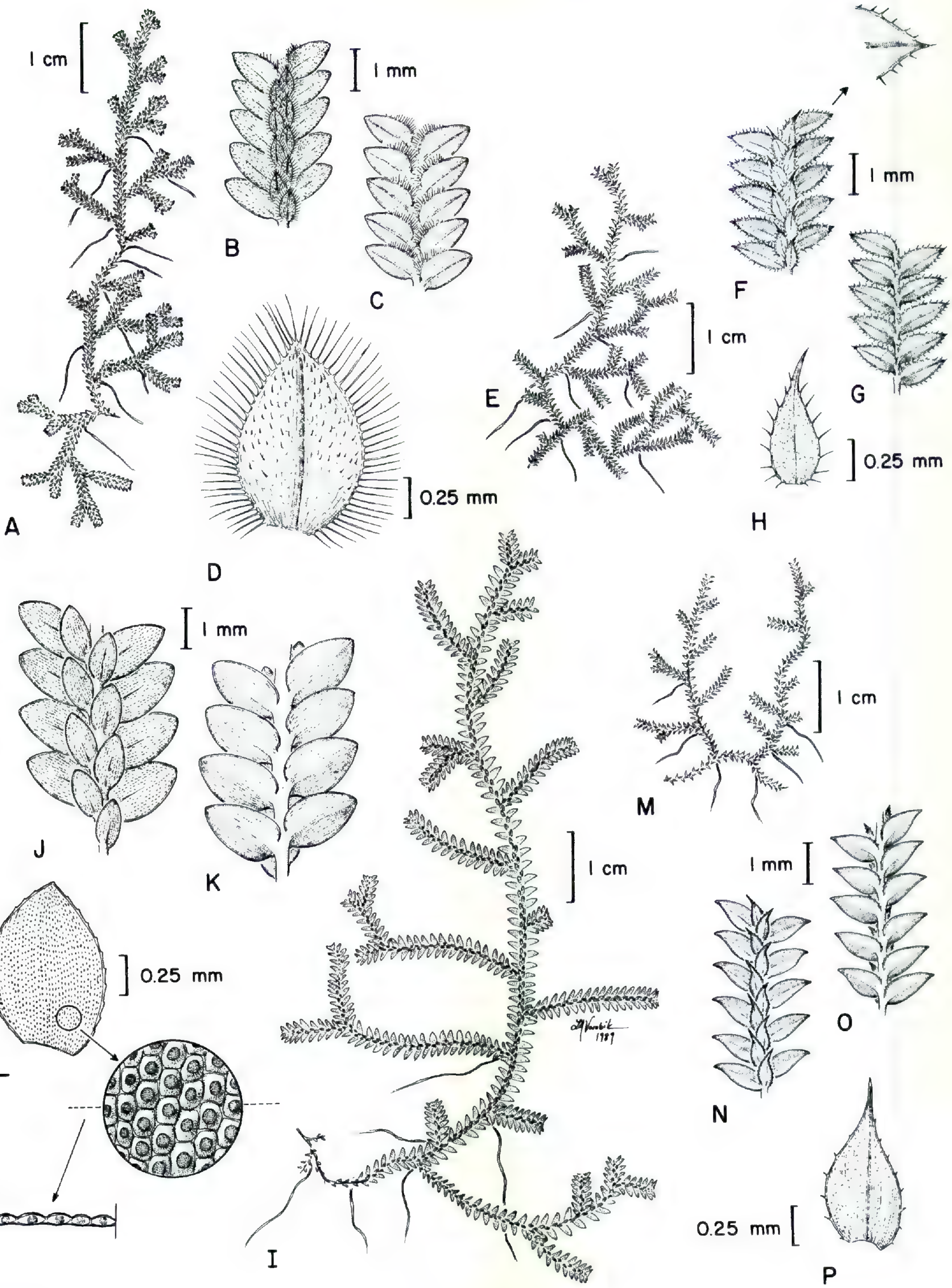

FIGURE 8. New species of *Selaginella*. A–D. *Selaginella velutina, Huber 12566*, UC.—A. Habit.—B. Adaxial surface.—C. Abaxial surface.—D. Adaxial surface of median leaf. E–H. *Selaginella breweriana, Beitel 85310*, UC.—E. Habit.—F. Adaxial surface.—G. Abaxial surface.—H. Adaxial surface of median leaf. I–L. *Selaginella beitelii, Beitel 85079*, UC.—I. Habit.—J. Adaxial surface.—K. Abaxial surface.—L. Adaxial surface of median leaf with surface and cross-section details. M–P. *Selaginella neblinae, Boom & Weitzman 5848*, UC.—M. Habit.—N. Adaxial surface.—O. Abaxial surface.—P. Adaxial surface of median leaf.

stem tips. The bluish green color of the leaves, reported in a number of *Selaginella* species, seems to be a function of the way light is reflected from the papillate cell surfaces, a feature that can be seen in dried material at 30× magnification.

Selaginella breweriana A. R. Smith, sp. nov.
TYPE: Venezuela. Territorio Federal Amazonas: Cerro de la Neblina, Camp 11, 6.2 km NNE Pico Phelps, Caño Beitel, 0°51′45″N, 65°58′52″W, 1,600 m, 28 Feb. 1985, *Beitel 85310* (holotype, UC; isotype, NY not seen). Figure 8E–H.

Caules repentes, usque ad 0.2 mm diam., non articulati, apicibus flagelliformibus et sobolibus carentes, rhizophoris filiformibus 0.1 mm diam. per totam longitudinem caulis praediti; folia ubique dimorpha, membranacea, utrinque glabra; folia intermedia ovato, marginibus albidis carentia, usque ad ca. 0.8 × 0.4 mm, ad apicem acuminata vel aristata, secus margines ciliata, ciliis 0.1–0.2 mm; folia lateralia usque ad ca. 1.3 × 0.7 mm, ad apicem acuminata vel breviaristata, secus margines ciliata, ciliis 0.1–0.2 mm.

Plants forming mats on rock, branch system anisotomous and ca. 3 or 4 times divided, branches arising all along main stems, these not much differentiated from the lateral ones; stems up to 0.2 mm diam., prostrate, lacking flagelliform tips or sobols, nonarticulate, bearing filiform rhizophores 0.1 mm diam. along their length; leaves dimorphous throughout, dark gray-green adaxially, lighter green abaxially, thin-textured, glabrous on both surfaces; medial leaves ovate-acuminate, lacking a whitish border, to ca. 0.8 × 0.4 mm, aristate at apex, ciliate along both margins, cilia 0.1–0.2 mm; lateral leaves to ca. 1.3 × 0.7 mm, rounded at the base, acuminate or short-aristate at apex, ciliate along both margins, cilia 0.1–0.2 mm, slightly longer along acroscopic margin; sporophylls not seen.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro de la Neblina, Camp 10, 12.5 km NNW of Pico Phelps, 0°54′30″N, 66°02′30″W, 1,670–1,690 m, 13 Feb. 1985, *Boom & Weitzman 5846* (NY not seen, UC).

This is perhaps most closely related to *S. schultesii* Alston ex Crabbe & Jermy but differs in having the lateral leaves basiscopically ciliate and in the absence of a white border on the medial leaves. It is also similar to *S. brevifolia* Baker, which has shorter-aristate, more broadly ovate, and more strongly keeled median leaves and minute hairs along the basiscopic surface of the lateral leaves. From *S. velutina* A. R. Smith and *S. valdepilosa* Baker, two other allies of similar habit, it differs in the aristate median leaves.

Selaginella cyclophylla A. R. Smith, sp. nov.
TYPE: Venezuela. Territorio Federal Amazonas: Dpto. Atures, Río Coro-Coro, W of Serranía de Yutaje, 6 km N of settlement of Yutaje, 05°44′N, 66°07′30″W, on rocks near base of waterfall, 320 m, 22 Feb. 1987, *Liesner & Holst 21304* (holotype, UC; isotype, MO not seen). Figure 9A–D.

Caules repentes, usque ad 0.3 mm diam., non articulati, apicibus flagelliformibus et sobolibus carentes, rhizophoris filiformibus 0.1 mm diam. per totam longitudinem caulis praediti; folia fere monomorpha in amplitudine sed dimorpha in dispositione, membranacea, glabra; folia intermedia fere rotundata vel suboblonga, margine albido carentes, ca. 0.7–0.8 × 0.6–0.7 mm, ad apicem rotundata, eciliata; folia lateralia usque ad ca. 1.0 × 0.8 mm, ad apicem rotundata, eciliata; sporophylla ovata, ca. 1 mm longa, pauca, laxe aggregata.

Plants forming mats on rocks or in crevices, branch systems anisotomous and 2 or 3 times divided, branches arising all along main stems, these not much differentiated from the lateral ones; stems up to 0.3 mm diam., prostrate, lacking flagelliform tips or sobols, nonarticulate, bearing filiform rhizophores 0.1 mm diam. along their length; leaves all about the same size but dimorphous in orientation, thin-textured, glabrous on both surfaces; medial leaves ± round or slightly oblong, lacking a whitish border, ca. 0.7–0.8 × 0.6–0.7 mm, rounded at apex, eciliate along margins; lateral leaves to ca. 1.0 × 0.8 mm, rounded at the base and apex, eciliate along both margins; sporophylls ovate, ca. 1 mm long, loosely clustered at the tips of short side branches; spores not seen.

Paratype. Same locality as type, in crevice below waterfall, *Liesner & Holst 21355* (UC, MO not seen).

The affinities of this very distinct species are uncertain; it has the same aspect as several other small-leaved species in Guayana, e.g., *S. rhodostachya* Baker and *S. valdepilosa* Baker but differs from these and others in one or more of the following characters: round or only slightly oblong median and lateral leaves; leaves rounded at the tip; leaves glabrous on both surfaces; and eciliate leaf margins.

Selaginella imbricans A. R. Smith, sp. nov.
TYPE: Venezuela. Territorio Federal Amazonas: Cerro de la Neblina, Río Yatua, mixed montane forest on talus between Camps 3 and 4, 700–900 m, 7 Nov. 1957, *Maquire et al. 41995* (holotype, UC). Figure 9K–N.

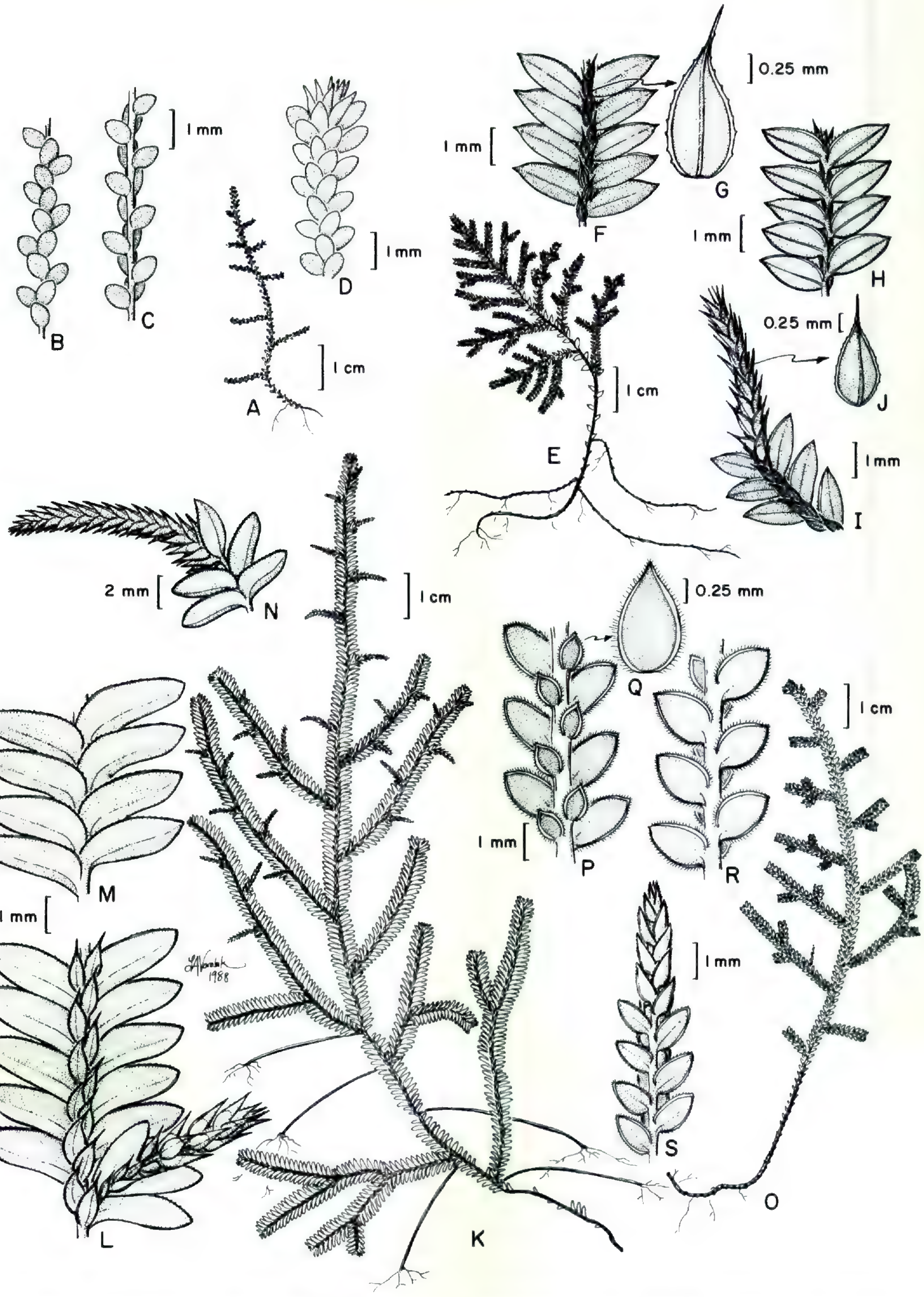

FIGURE 9. New species of *Selaginella*. A–D. *Selaginella cyclophylla, Liesner & Holst 21304*, UC.—A. Habit.—B. Adaxial surface.—C. Abaxial surface.—D. Fertile portion. E–J. *Selaginella sobolifera, Maguire & Politi 27331*, UC.—E. Habit.—F. Adaxial surface.—G. Median leaf.—H. Abaxial surface.—I. Fertile portion.—J. Sporophyll. K–N. *Selaginella imbricans, Maguire et al. 41995*, UC.—K. Habit.—L. Adaxial surface.—M. Abaxial surface.—N. Fertile portion. O–S. *Selaginella thysanophylla, Steyermark et al. 109121*, US.—O. Habit.—P. Adaxial surface.—Q. Median leaf.—R. Abaxial surface.—S. Fertile portion.

Differt a *S. producta* et speciebus affinibus foliis lateralibus imbricatioribus et oblongioribus, caulibus principalibus minus ramosis sed ramis valde regularibus, strobilis distinctissimis ex ramis primariis lateraliter gestis.

Plants creeping on rocks and boulders, branch systems anisotomous and 2 or 3 times divided, branches alternately arising all along main stem; stems up to ca. 0.7 mm diam., prostrate or ascending at the tip, lacking flagelliform tips or sobols, nonarticulate, bearing stoutish rhizophores to 0.5 mm diam. along their length; leaves dimorphous throughout, dark green on both sides, chartaceous, glabrous on both surfaces; medial leaves narrowly ovate-acuminate, lacking a whitish border, to ca. 2.0 × 0.6 mm, aristate at apex, denticulate along both margins; lateral leaves to 4.0 × 1.5 mm, rounded at the base and apex or subacute at tip, denticulate along the margins, especially the acroscopic one, teeth 0.05 mm or less; sporophylls borne laterally on the side branches and laterally along the sides of main stem toward the tip, arranged in distinct strobili, these 5–8 × 1.5 mm; microspores orangish; megaspores cream-colored.

Paratype. Same general locality as type, high montane forest south of Camp 3, 800–1,600 m, 24 Dec. 1953, *Maguire et al. 36885* (UC).

This species seems related to *S. producta* Baker and allies, to which it will key in Alston et al. (1981), but it differs in the more oblong, closely placed, even overlapping lateral leaves, the strobili tending to be produced as distinct side branches from the main lateral branches, and the more regularly but less-branched plant body. In habit, *S. imbricans* resembles *S. truncata* Karsten ex A. Braun, which is distinguished by the subacute or only slightly cuspidate median leaves.

Selaginella marahuacae A. R. Smith, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dpto. Atabapo, open rocky Plateau of Cerro de Marahuaca above Salto Los Monos on tributary of headwaters of Río Iquapo, 03°37′N, 65°23′W, 2,555 m, 26 Feb. 1985, *Liesner 18008* (holotype, UC; isotype, MO not seen). Figure 7F–I.

Differt a *S. potaroensi* Jenman foliis intermediis plus minusve symmetricis et acutis vel acuminatis, pagina adaxialis foliorum lateralium secus marginem basiscopicum glabra.

Plants of bluffs and rocky ledges, to ca. 15 cm, branch systems anisotomous and ca. 1–3 times divided, branches arising from all along length of main stem; main stems ca. 0.5 mm diam., creeping throughout but the branches sometimes ascending, nonarticulate, bearing filiform rhizophores ca. 0.2 mm diam. along the entire length; leaves dimorphous throughout, dark greenish above, lighter green below, chartaceous; medial leaves ovate, to ca. 1.8 × 1.4 mm, acute to acuminate at apex, rounded to truncate at base, denticulate along margin; lateral leaves ovate-oblong, 3–4 × 1.3–2.0 mm, acutish at tip, rounded at base, entire to minutely denticulate on margin, glabrous on both sides; strobili to ca. 6 × 3 mm, borne at tips of lateral branches; sporophylls uniform, ovate, somewhat spreading; megasporangia not basal, few; megaspores ca. 300 μm diam., cream-colored; microspores orangish, shed singly.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dpto. Atabapo, Cerro Marahuaca, cumbre, sección suroriental, vecindades del zanjón, 03°37′N, 65°21′W, 2,685 m, 15 Jan. 1981, *Maguire et al. 65673, 65674* (MO); Cerro Marahuaca, summit on SE corner, 3°37′N, 65°21′W, 2,700 m, 13–14 Oct. 1988, *Liesner 24806* (UC).

Most similar to *S. potaroensis* Jenman and *S. muscosa* Spring in C. Martius, which differ by having aristate medial leaves. From the former, *S. marahuacae* also differs in the more or less symmetrical medial leaves and absence of minute hairs along the basiscopic adaxial margin. This new species grows at much higher elevations than either of its close relatives, which are known almost entirely from below 1,500 m.

Selaginella neblinae A. R. Smith, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Cerro de la Neblina, Camp 10, 12.5 km NNW of Pico Phelps, 0°54′30″N, 66°02′30″W, 1,670–1,690 m, 13 Feb. 1985, *Boom & Weitzman 5848* (holotype, UC; isotype, NY not seen). Figure 8M–P.

Differt a *S. rhodostachya* Baker foliis lateralibus acutis ovato-lanceolatis, foliis intermediis breviaristatis; a *S. breweriana* foliis intermediis et lateralibus eciliatis vel breviter ciliolatis dignoscenda.

Plants forming mats on wet rocks or on rock faces near streams and waterfalls, branch systems anisotomous and ca. 2 or 3 times divided, branches arising all along main stems and not much differentiated from them; stems up to 0.2 mm diam., prostrate, lacking flagelliform tips or sobols, nonarticulate, bearing filiform rhizophores 0.1 mm diam. along their length; leaves dimorphous throughout, yellowish green, thin-textured, glabrous on both surfaces; medial leaves ovate-acuminate, lacking a whitish border, to ca. 0.8 × 0.4 mm, aristate at apex, ciliolate along both margins,

cilia 0.05–0.1 mm; lateral leaves to ca. 1.3 × 0.7 mm, rounded at the base, acute at apex, entire, denticulate, or the largest ones short-ciliolate along acroscopic margin, cilia ca. 0.05 mm; sporophylls ovate, to ca. 1 mm, denticulate or ciliolate along the margin; microspores orangish, shed singly; megaspores not seen.

Paratype. Same locality and date as type, *Boom & Weitzman 5824* (UC, NY not seen).

This species is similar to *S. rhodostachya* Baker but differs by having acute, ovate-lanceolate lateral leaves and short-aristate median leaves. It is also similar to *S. breweriana*, which differs by the long-ciliate median and lateral leaves.

Selaginella pubens A. R. Smith, sp. nov.
TYPE: Venezuela. Territorio Federal Amazonas: Cerro Sipapo (Paráque), above Upper Camp Savanna, 1,800 m, 12 Dec. 1948, *Maguire & Politi 27634* (holotype, UC; isotype, NY not seen). Figure 7N–R.

Ex affinitate *S. tyleri* A. C. Smith et *S. hirsutae* Alston ex Crabbe & Jermy, ab ambabus caulibus primariis repentibus ramis ascendentibus, caulibus gracilioribus usque ad 0.8 mm diam. distincta; differt a *S. hirsuta* foliis adaxialiter pilosis.

Plants on moist rocks and cliffs, to 12 cm, branch systems anisotomous and ca. 4 or 5 times divided, branches arising along length of main stem; main stems to 0.8 mm diam., creeping but with ascending branches, nonarticulate, bearing filiform rhizophores 0.2–0.3 mm diam. along their length; leaves dimorphous throughout, dark green and shining, firm; medial leaves ovate, ca. 1.5 × 1.0 mm, acuminate at apex, rounded to truncate and with a tuft of hairs 0.2–0.3 mm at the outer base, with dense adpressed hairs 0.1 mm on adaxial surface; lateral leaves oblong-ovate, to ca. 2.5 × 1.0 mm, partially twisted away from the plane of branching system, basiscopic margin inrolled, ciliate along acroscopic margin with hairs to ca. 0.15 mm, bearing hairs 0.1 mm on both surfaces, those of adaxial surface adpressed; strobili tetragonous, to ca. 4 × 1.5 mm at tips of lateral branch systems; sporophylls ovate, ca. 1.4 mm long and nearly as broad, denticulate on margin; megaspores ca. 300 μm diam., light yellowish or cream-colored, with low rugose ridges; microspores light orange, shed singly, papillate or with capitate projections.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro Sipapo (Paráque), between Phelps Camp and North Savanna, 1,400 m, 17 Dec. 1948, *Maguire & Politi 27749* (UC).

This species is most closely related to two others that also have pubescent leaf surfaces, *S. tyleri* A. C. Smith and *S. hirsuta* Alston ex Crabbe & Jermy. These two both differ in their erect habit and stouter (to 2 mm diam.) stems. Both have an erect main stem with a lateral branching system that begins well up from the stem base. In addition, *S. tyleri* differs in having a regularly pinnate branching system and having the ultimate divisions several cm long. *Selaginella hirsuta* has adaxially glabrous leaves.

Selaginella sobolifera A. R. Smith, sp. nov.
TYPE: Venezuela. Territorio Federal Amazonas: Río Cuao, Río Orinoco, Danta (Tapir) Falls, moist woodland, 125 m, 19 Nov. 1948, *Maguire & Politi 27331* (holotype, UC; isotype, NY not seen). Figure 9E–J.

Caules primarii erecti, usque ad ca. 0.8 mm diam., nec articulati nec apicibus flagelliformibus, infra ramos infimos sobolibus filiformibus usque ad 5 cm × 0.15 mm et rhizophoris sparsis 0.1 mm diam. praediti; folia ubique dimorpha, chartacea, utrinque glabra; folia intermedia ovato-lanceolata, usque ad ca. 1.0 × 0.3–0.4 mm, margine denticulata et anguste sed clare albida, ad apicem longiaristata; folia lateralia usque ad ca. 2.0 × 1.0 mm, ad apicem acuta, basi ciliolata secus marginem acroscopicum; sporophylla lanceolata, margine denticulata; strobili usque ad ca. 6 × 1.5 mm.

Plants ± erect, branch systems anisotomous and ca. 2 or 3 times divided, branches alternately arising along the main stem beginning 3–5 cm above the prostrate portion; main stems to ca. 0.8 mm diam., stramineous, nonarticulate, lacking flagelliform tips, bearing sparse, filiform rhizophores 0.1 mm diam., also with more numerous threadlike sobols (runners) to 5 cm long or more along the unbranched portion, these 0.15 mm diam., bearing minute, ascending leaves ca. 0.3–0.4 mm long; leaves dimorphous throughout, green on both sides, thin-textured, glabrous on both surfaces; medial leaves ovate-lanceolate, with a narrow but distinct whitish border, to ca. 1.0 × 0.3–0.4 mm, long-aristate at the tip, arista ca. half the length of the main body of the leaf, denticulate along the margins; lateral leaves to ca. 2.0 × 1.0 mm, rounded at the base, acute at apex, ciliolate along the acroscopic basal margin, the cilia ca. 0.1 mm; sporophylls lanceolate, white-bordered, denticulate on the margin, curving outward, arranged in strobili up to ca. 6 × 1.5 mm; megasporangia not seen; microsporangia containing orangish microspores.

Closest relatives of this new species are uncertain. In Alston et al. (1981), it will key to near *S. cladorrhizans* A. Braun, which has a more creep-

ing habit, lacks sobols, and has flagelliform branch apices. Of Venezuelan species, *S. sobolifera* has more prominent sobols than any other species.

Selaginella thysanophylla A. R. Smith, sp. nov.
TYPE: Venezuela. Bolívar: Meseta del Jaua, Cerro Sarisariñama, porción nor-este, interior y fondo arboreado de la Sima Mayor, 4°41′40″N, 64°13′20″W, 700 m, 12–15 Feb. 1974, *Steyermark et al. 109121* (holotype, US). Figure 9O–S.

Caules primarii erecti, ca. 0.6 0.8 mm diam., non articulati, nec apicibus flagelliformibus nec sobolibus, basi rhizophoris paucis ca. 0.2 mm diam.; folia dimorpha supra ramos infimos, infra ramos fere monomorpha et ascendentes, chartacea, glabra; folia intermedia ovata, usque ad ca. 1.4 × 1.0 mm, ad apicem apiculata, dense fimbriata in margine, ciliis ca. 0.3 mm, margine foliorum manifeste albido; folia lateralia ovata, usque ad ca. 2.0 × 1.5 mm, manifeste fimbriata ad marginem albidum; strobili ca. 2–3 × 1.2 mm, indistincti.

Plants erect from short-creeping and then upward-curving stems, branch systems anisotomous and 2 or 3 times divided, branches arising along the main stem 4–8 cm above the prostrate and rhizophore-bearing portion; main stems 0.6–0.8 mm diam., erect, lacking flagelliform tips or sobols, nonarticulate, bearing a few filiform rhizophores ca. 0.2 mm diam. toward the base (these only on prostrate or curved-ascending portion); leaves dimorphous above the first branches, below that rather uniform, lowest ones of main stem all strongly ascending and clasping the stem, dark green adaxially, lighter green abaxially, chartaceous, glabrous on both surfaces; medial leaves ovate, with a very distinct whitish border ca. 0.1 mm wide, to ca. 1.4 × 1.0 mm, apiculate at the apex, very densely long-ciliate along margins, cilia to ca. 0.3 mm; lateral leaves ovate, to ca. 2.0 × 1.5 mm, with a distinct whitish border ca. 0.05 mm wide, rounded at the base, rounded to subacute at the tip, densely ciliate along both margins, cilia to ca. 0.3 mm; sporophylls in indistinct strobili ca. 2–3 × 1.2 mm at the tips of side branches; megasporangia producing light yellowish megaspores ca. 150 μm diam.; microsporangia producing orangish microspores that are shed singly.

This is a most distinct new species without obvious close relatives. The broad whitish border of the prominently fringed leaves is reminiscent of *S. pallescens* (C. Presl) Spring, and this species may be a close relative.

Selaginella velutina A. R. Smith, sp. nov. TYPE: Venezuela. Bolívar: Mun. Gran Sabana, Meseta del Auyan-Tepuí, sector noroccidental, aprox. 2 km al NE de la Sima Ahonda, 6°02′N, 62°36′W, 1,600 m, 29 Feb. 1988, *Huber 12566* (holotype, UC; isotype, MYF not seen). Figure 8A–D.

Caules repentes, ca. 0.2 mm diam., non articulati, nec apicibus flagelliformibus nec sobolibus, rhizophoris filiformibus 0.1 mm diam. per totam longitudine caulis praediti; folia ubique dimorpha, membranacea, adaxialiter pilis dentis antrorsis ca. 0.1 mm longis; folia intermedia ovata, ca. 1.0 × 0.5 mm, ad apicem acuta, dense ciliata ad marginem virellum, ciliis usque ad 0.3 mm; folia lateralia ovata, usque ad 1.5 × 1.0 mm, ad apicem subacuta, ad marginem acroscopicum dense longiciliata, ciliis usque ad 0.5 mm, ad marginem basiscopicum ciliolata, ciliis ca. 0.1 mm.

Plants forming colonies in moist, shady crevices, branch systems anisotomous and ca. 3 times divided; main stems ca. 0.2 mm diam., creeping, nonarticulate, bearing filiform rhizophores 0.1 mm diam. along their length; leaves dimorphous throughout, dark gray-green adaxially, lighter green abaxially, dull, thin-textured, both the medial and lateral ones with dense, short, curved, antrorse hairs ca. 0.1 mm adaxially; medial leaves ovate, ca. 1.0 × 0.5 mm, truncate at the base, acute at apex, densely ciliate on both margins, cilia to 0.3 mm, prominent whitish border lacking; lateral leaves ovate, to ca. 1.5 × 1.0 mm, rounded at the base, subacute at apex, densely long-ciliate on acroscopic margin with hairs to 0.5 mm, weakly short-ciliate on basiscopic margin, hairs ca. 0.1 mm; sporophylls not seen.

This is a most distinct new species, and I am uncertain of its closest relatives. In size and shape of the leaves, it resembles *S. valdepilosa* Baker but differs in the densely pubescent adaxial surface of the median and lateral leaves and in the denser cilia on the margins of the leaves. From other species that have hirsute leaf surfaces, e.g., *S. tyleri* A. C. Smith and *S. pubens* A. R. Smith, *S. velutina* differs in its more prostrate habit and thinner leaves, with the medial ones merely acute at the apex.

Selaginella versatilis A. R. Smith, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Cerro Sipapo (Paráque), rim head of South Basin, 2,100 m, 26–28 Jan. 1949, *Maguire & Politi 28652* (holotype, UC; isotype, NY not seen). Figure 10.

Caules scandentes usque ad 2.5 mm, usque ad 1.5–3.0 mm diam., non articulati, adaxialiter 2-porcati, pilis sparsis vel densis crispatis 0.2–0.4 mm praediti; rami ex

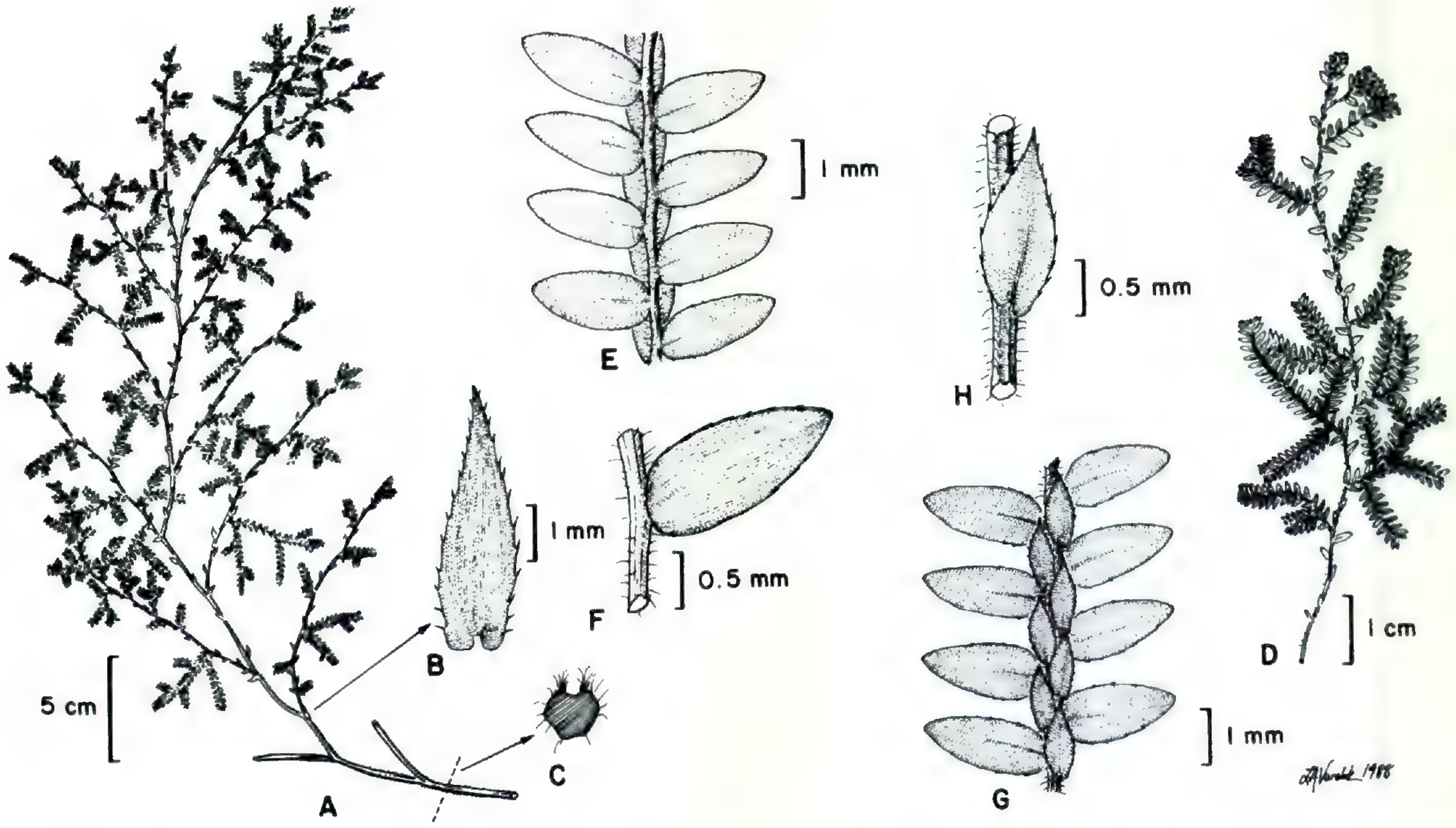

FIGURE 10. *Selaginella versatilis, Maguire & Politi 28652*, UC.—A. Portion of branching system.—B. Older stem leaf.—C. Cross section of stem, with adaxial ridges.—D. Ultimate portion of branching system.—E. Abaxial surface.—F. Lateral leaf.—G. Adaxial surface.—H. Median leaf.

rhachidi valde flexuosa alternatim orienti, rhizophoris longis crassis ca. 1 mm diam. praediti; folia ubique dimorpha, chartacea, utrinque glabra; folia intermedia elliptica, plerumque 3–5 × 1 mm, basi biauriculata, auriculis fere aequalibus, ad apicem acuta, ad marginem dentibus in pilos terminatibus; folia lateralia elliptica, 3–5 × 1 mm, basi non auriculata, ad apicem acuta, ad marginem dentibus remotis usque ad 0.5 mm; folia axillaria elliptico-lanceolata, non auriculata; megasporangia ut videtur basales.

Plants on open breaks, climbing and sprawling over shrubs and tree bases, to 2.5 m, branch systems anisotomous and 3 or 4 times divided, branches arising from all along length of main stem; main stems 1.5–3.0 mm diam., stramineous, suberect or leaning on other vegetation, with 2 adaxial angular ridges creating an adaxial groove, with scattered to dense ± flexuous hairs 0.2–0.4 mm, these most prominent along adaxial groove; branches arising alternately from a zig-zag rachis, ascending, nonarticulate, bearing long, stout rhizophores ca. 1 mm diam. along much of their length, these arising adaxially; leaves dimorphous throughout, blue-green when living, green when dried, chartaceous; medial leaves elliptic, mostly 1.5–5 × 1 mm, acute to acuminate at apex, biauriculate at base, the auricles ± equal, margin with teeth tipped by a hair, the teeth multicellular at their base, mostly 0.1–0.3 mm; lateral leaves elliptic, 3–5 × 1 mm, acutish at tip, narrowed and nonauriculate at base, the margin with scattered teeth from a multicellular base to 0.5 mm; axillary leaves elliptic-lanceolate, not auriculate; mature sporophylls not seen; megasporangia evidently basal.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: cumbre del Cerro Autana, bosque bordeando la cima de la parte escarpada del lado noreste, 1,230–1,270 m, 21–22 Sep. 1971, *Steyermark 105156* (MO, US—4 sheets); Cerro Marahuaca, upstream from "Sima Camp," along branch of Caño Negro, south-central portion of meseta, 03°43′N, 65°31′W, 22 Feb. 1985, *Steyermark & Holst 130581* (MO, UC).

This remarkable new species is without close relatives, but, even though it lacks swollen nodes or articulations, it appears to be most closely allied to such articulate species as *S. anaclasta* Alston ex Crabbe & Jermy, as suggested by the sparingly toothed leaves tipped with hairs. Other relatives may be *S. asperula* Spring in C. Martius and *S. coarctata* (Arn.) Spring in C. Martius, which also lack stem articulations. This affinity is suggested by the hairy stems, shown sparingly in the type and more densely in *Steyermark & Holst 130581*. None of the collections seen have mature strobili, but a few sheets of *Steyermark 105156* show incipient strobili with basal megasporangia. The biauriculate medial leaves and adaxially arising rhizophores also indicate affinity with the articulate group.

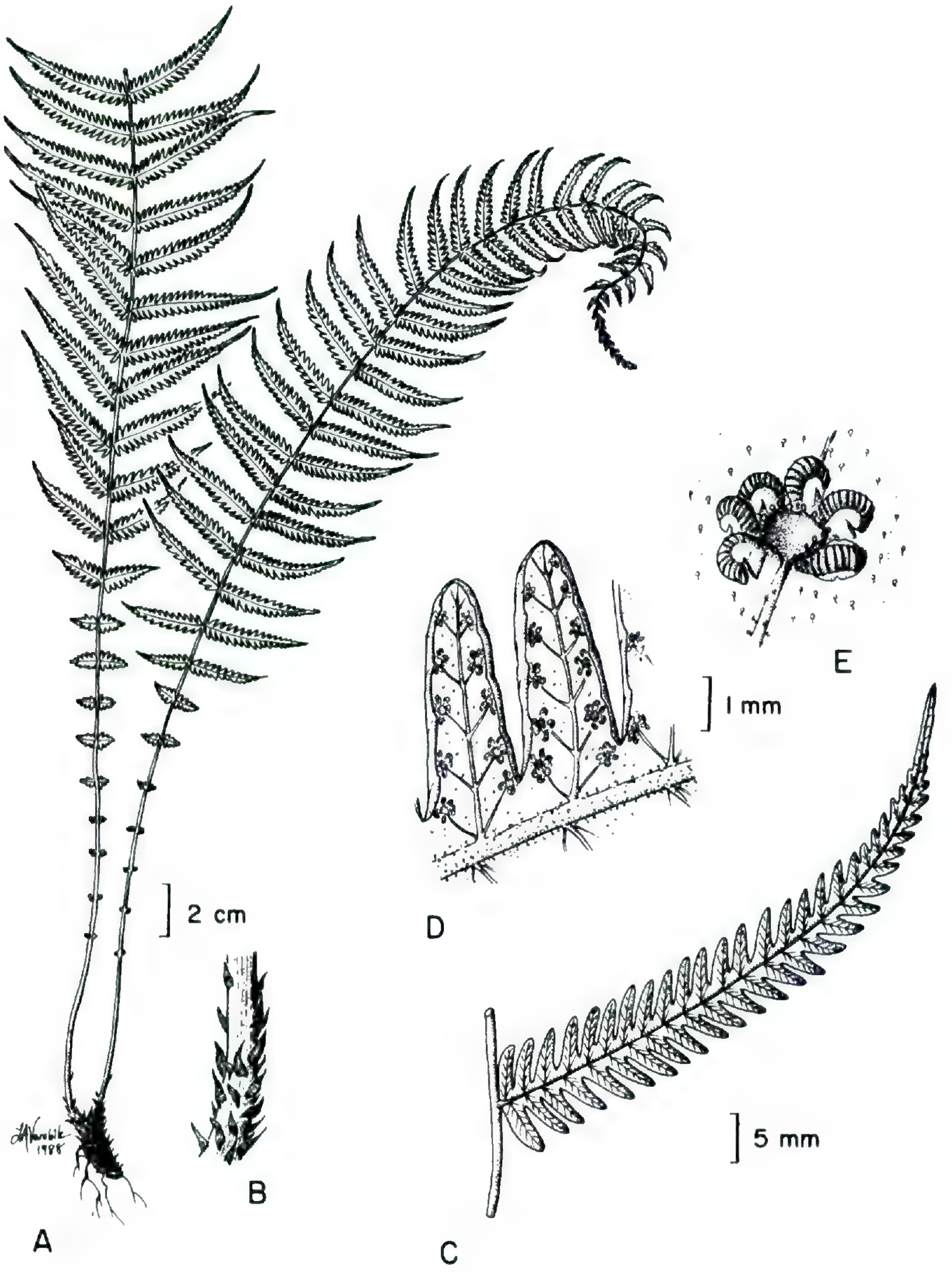

FIGURE 11. *Thelypteris peradenia*, based on *Im Thurn 94* and *380*, K.—A. Habit.—B. Stipe base.—C. Pinna.—D. Segments, abaxial surface.—E. Sorus with indusium.

THELYPTERIDACEAE

Thelypteris (subg. **Amauropelta**) **peradenia** A. R. Smith, sp. nov. TYPE: Venezuela [British Guiana on label.] Bolívar: Mt. Roraima, *Im Thurn 94* (holotype, K). Figure 11.

Ex affinitate *T. oppositae* (Vahl) Ching et specierum affinium lamina epilosa, abaxialiter abundanter stipitato-glandulosis, pinnis incisioribus distinguenda.

Rhizome suberect; fronds ca. 50 cm; stipe 4–6 cm × 1.5–2.0 mm, epilose, at base with ovate-lanceolate, brown, glabrous scales to 5 × 2 mm; lamina coriaceous, ca. 45 cm, proximally with ca. 9–12 pairs of gradually reduced pinnae, lowermost vestigial and ca. 1 mm long or less; aerophores lacking, but rachis swollen at point of pinna attachment; pinnae opposite to subopposite, lanceolate, to 6 × 1.2 cm, incised to ca. 1 mm from costa; segments linear-lanceolate, 2.0–2.5 mm wide at sinus, oblique, margins inrolled; indument abaxially of light yellow stipitate glands on rachis, costae, veins, and laminar tissue, hairs lacking, also with a few sessile, orangish glands along costules and laminar tissue, adaxially with scattered stipitate glands, veins impressed; sori supramedial, indusia with stipitate glands, persistent.

Paratype. Specimen mounted on same sheet as holotype and from same general locality, upper slope of Roraima, Dec. 1884, *Im Thurn 380* (K).

This is most closely related to *T. opposita* and allies but differs by having more incised pinnae with linear-lanceolate segments, copiously stipitate-glandular lamina abaxially, less obvious sessile resinous glands abaxially, and complete lack of hairs.

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OBSERVATIONS ON *CTENITIS* (DRYOPTERIDACEAE) AND ALLIED GENERA IN AMERICA

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ABSTRACT

A brief taxonomic history of the fern genus *Ctenitis* is traced from its status as a subgenus of *Dryopteris* (Christensen, 1920) to its elevation to generic rank and the recent separation from it of *Megalastrum* and *Triplophyllum*. A key to the three genera is provided, and a comparison is made by the author of his treatment of species in *Ctenitis* s. lat. in *The Ferns and Fern Allies of Guatemala* with the same genus narrowly defined in *Pteridophyta of Peru* (in prep.). Traditional, as well as little used diagnostic features are listed, compared, and assessed, in an attempt to determine which will be the most reliable, in correlation with others, for ascertaining species relationships. These are employed in a preliminary analysis of the three remaining groups of Christensen's *Ctenitis* s. str. (*ampla*, *hirta*, *submarginalis*), and suggestions are made as to correlation of characters in future studies of the genus.

Carl Christensen's work on dryopteroid ferns (1913, 1920) was vital to New World fern taxonomy in two ways. First, he assembled all the American species which previously had been placed in the genus *Dryopteris* Adanson. Concurrently, by aligning the species into subgenera, he underscored significant differences between some of the groups. This then focused attention upon these subgenera so that later authors, with the help of newer collections and studies of spore morphology, have been able to elevate some of the species groups to generic status.

Christensen (1938, p. 544) elevated his subgenus *Ctenitis* to generic rank, a choice promptly and generally accepted by pteridologists. Recently Tryon & Tryon (1982) reaffirmed the validity of most of Christensen's species groups of *Ctenitis* by including them in their key to the genus. They also reinforced or realigned them and added new observations on spore characters. Holttum elevated one of Christensen's species groups of subg. *Ctenitis* to the new genus *Triplophyllum* Holttum (1986a) and another to *Megalastrum* Holttum (1986b). He indicated that *Triplophyllum* is less closely allied to *Ctenitis* than it is to *Tectaria* Cav. In support of Holttum, Smith & Moran (1987) pointed out that *Ctenitis* is more closely related to *Lastreopsis* Ching than to *Megalastrum* and published 39 new combinations of species of the latter.

ARTIFICIAL KEY TO AMERICAN GENERA CLOSELY RELATED TO *CTENITIS*

1a. Stem long-creeping, the leaves borne at intervals; lamina commonly deltoid-pentagonal (at least in the Neotropics), i.e., the basal pinnae conspicuously longer than adjacent ones and usually more than half as long as the rest of the lamina; scales of petiole base 1–4 mm long, not abundant; scales of costae and rachis few or none; spores with winglike ridges ..... *Triplophyllum*

1b. Stem decumbent to erect, the leaves caespitose; lamina not deltoid-pentagonal, the basal pinnae shorter than to slightly longer than adjacent ones (although basal ones much broader and more dissected in *C. hemsleyana*); scales of petiole base 6–30 mm long, abundant, often in dense clusters (but shorter and less abundant in *Ctenitis nigrovenia*); scales of costae and rachis ample to abundant; spores lacking winglike ridges (although in *Ctenitis* sometimes with broad folds that under the light microscope may appear winglike) 2

2a. Axes adaxially bearing reddish brown trichomes ("*Ctenitis*-hairs"), these with 2–4 cells and less than 0.4 mm long, drying in a catenate state, and usually with blunt tips; vein tips slender; basal basiscopic vein of distal pinnules arising from costule (or very close to its juncture with the costa) ..... *Ctenitis*

2b. Axes adaxially bearing whitish trichomes with usually more than 4 cells, 0.5 mm or longer, drying terete or flat, and with pointed tips; vein tips conspicuously clavate; basal basiscopic vein of distal pinnules definitely arising from the costa ..... *Megalastrum*

Holttum (1985) and Smith & Moran (1987) adequately described most of the diagnostic features of *Triplophyllum* and *Megalastrum*, but a similar consideration of the American species remaining in *Ctenitis* has yet to be published. I recently completed treatments for all three genera for *Pteridophyta of Peru* in a current collaboration

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with Rolla Tryon (in prep.) and strongly affirm the distinctiveness of each. Treatment of *Ctenitis* s. lat. in Guatemala (Stolze, 1976) provided insight into problems of Central American species. Recent studies of specimens from Peru and adjacent areas, including a great number of types, allowed me to assess the relative value of the most significant characters of *Ctenitis* s. str. This served as an interesting comparison of species and species complexes common to both regions. Furthermore, during both studies most species from the rest of the Neotropics and subtropical South America were examined in the search for additional correlating characters. At this point it seems expedient to highlight equivalent diagnostic characters that need to be considered in future floristic or monographic treatments of *Ctenitis* s. str. which, even in the new, narrowed circumscription, is still in great need of revision. Despite Christensen's excellent work, relationships of species in his major remaining groups are suspect, and a fresh approach is needed in their evaluation. It is the author's intent here to compare and evaluate features traditionally and/or newly employed in the genus to separate species, to point out those that are most effective, and, conversely, to caution against reliance on those that are likely too variable to be effective. A search for correlation of the strongest characters needs to be pursued in order to ascertain true species relationships.

Sori

Soral position can be constant in some species and variable in others, thus it is not a good character for separating major species complexes. For example, sori in *Ctenitis refulgens* (Mett.) Vareschi (Mexico, South America) and *C. grisebachii* (Baker) Ching (Central America, Greater Antilles) are consistently inframedial, those of *C. equestris* (Kunze) Ching (Central America) and *C. excelsa* (Desv.) Proctor (Central America, Lesser Antilles) are medial to inframedial, yet the common *C. submarginalis* (Langsd. & Fisch.) Ching (Florida to Uruguay) has sori borne variably from near midvein to close to the margin.

Indusia

Among species that have conspicuous, persistent indusia are *C. melanosticta* (Kunze) Copel. (Mexico and Central America), *C. oophylla* (C. Chr.) Ching (Jamaica, Hispaniola), and *C. strigilosa* (Davenp.) Copel. (Mexico, Guatemala). Indusia are absent in *C. excelsa* and *C. refulgens*. They may only seem to be so in other species; for example, in *C. submarginalis* they are minute and fugacious and may be obscured by fully expanded sori on mature leaves. Occasionally, the condition may vary geographically, as in *C. nigrovenia* (Christ) Copel. (southern Mexico to Peru). In this species indusia are commonly small and subpersistent in Peru but fugacious throughout the rest of the range.

Indusia can be pubescent or glandular on the surface or margin, or glabrous. Indusial indument usually is a difficult character to assess, as it tends to be minute, scattered, and frequently obscured within the folds of mature indusia. Indusia in the South American *C. ampla* (Willd.) Ching are typically reddish glandular-pubescent, but the condition does not seem to be constant. A typical problem with this character is encountered in the original descriptions of *C. microchlaena* (Fée) Stolze (southern Mexico, Costa Rica, Colombia, Venezuela, Peru) and a synonym, *Dryopteris karstenii* (A. Braun) C. Chr. Indusia were described as glabrous and caducous in the former, and ciliate and persistent in the latter. However, examination of type material revealed that there is much more variation in indusia than described in the protologues, and this is uncorrelated with any other diagnostic feature.

Glands

Glands provide another subtle character in *Ctenitis* that is usually difficult to observe and can be a source of confusion. In a few species presence of glands is a strong diagnostic feature, such as in *C. oophylla*, where they are numerous and erect on the abaxial surface of segments. However, more frequently they are about 0.1 mm long, cylindrical, and appressed to the surface. In species where glands of this type are sparse and yellowish, and little contrasted with veins or tissue, they easily can be overlooked, especially at magnifications less than 30×.

On Guatemalan specimens of the common *C. submarginalis*, glands are sparse or lacking on abaxial surfaces. In southern Mexico, Smith (1981) and Mickel & Beitel (1988) reported yellow, cylindrical glands, but in Peru all specimens examined were eglandular. Although I did not see a type specimen, the type of a synonym, *Nephrodium tarapotense* Hooker (K), from Peru, is eglandular.

Glands on veins and costules of *C. ampla* are either conspicuous and reddish or lacking, although in *C. sloanei* (Sprengel) Morton (Neotropics), yellow glands are inconspicuous but persistent. The obvious conclusion is that, despite the fact that glands have been used in regional treatments as a

secondary character to delineate species of *Ctenitis*, much caution should be exercised in their observation and use. However, once subjected to more detailed analysis, the character may help define species groups.

Scales

Scale type traditionally has been one of the most effective characters used to separate groups and species of *Ctenitis*. Scales may vary among species in color, rigidity, breadth, shape, and margin. Those borne on the petiole can also differ from those elsewhere, e.g., on the rachis or costae. Although *Ctenitis* scales are generally and obviously clathrate, in a few species they are only scarcely so.

An often diagnostic character of some scales is the tendency for their margins to curve inward upon themselves and nearly touch, either throughout or at their base. Broader ones of this type appear to have an inflated aspect, which has been variously termed vaulted, bullate, or sub-bullate. Some species with conspicuous bullate scales, especially on the rachis and costae abaxially, are *C. lanceolata* (Baker) A. R. Smith (Fig. 1d), *C. oophylla*, and *C. salvinii* (Baker) Stolze. Many of these scales appear like little turbans or as balloons with attenuate tips. Contrasting greatly are those of *C. hemsleyana* (Hemsley) Copel. (southern Mexico, Central America), *C. refulgens*, and *C. strigilosa* (Fig. 1c), which on the axes are so long and narrow they resemble trichomes, yet at their very base are abruptly expanded or sub-bullate. This type of scale is generally abundant and deep brown or blackish, giving the petiole and rachis a dark and densely hairy appearance.

Although margins of scales vary in the genus from entire to remotely denticulate to ciliolate, subentire margins are the most common. Even where stem scale margins are more or less denticulate, scales up the petiole and onto the rachis often grade to entire. Authors have used this character to separate a few species, but usually it is too inconstant to serve as more than a minor diagnostic feature.

Typically, *Ctenitis* scales are somewhat lax and delicate, the cells broad and their walls thin—thus they are conspicuously clathrate (Fig. 1b). A few species have much more rigid scales, with narrow cells and very thick walls, hence they are scarcely clathrate. An example is *C. grisebachii* (Baker) Ching (Fig. 1e), with petiole scales so rigid and stout that the base persists on the petiole surface after the scale has been broken off. The effect is a very reddish muricate petiole. Although uncommon in the genus, this type seems to be constant, as well as distinctive, within species.

Trichomes

Trichome type is a major character in separating *Megalastrum* from *Ctenitis*, but it is of little help within the genus, except for the presence or absence of trichomes on segment margins. This subtle, often inconspicuous, character usually has been ignored in keys and descriptions of *Ctenitis*. The segment margins of many species are sparsely to amply provided with minute trichomes (Fig. 1a), in addition to others on the axes, veins, or surfaces. These trichomes are 0.1–0.3 mm long, articulate, with 2–4 cells, and dry in a catenate state. In species where they are more abundant, the margins appear under low magnification to be amply ciliate. In species where the trichomes are sparse, they may be found only in the area of segment sinuses. Although the condition is common throughout the genus, a few species are distinctive for the complete absence of marginal trichomes. Some examples are *C. lanceolata* (Baker) A. R. Smith and *C. salvinii* (Baker) Stolze (both southern Mexico, Guatemala), as well as *C. excelsa* and *C. nigrovenia*.

A very inconspicuous type of trichome is found in various species of *Ctenitis*, which also occurs in other genera of Dryopteridaceae. In certain species these trichomes are found abaxially on the minor axes and are so tiny they are often overlooked. Those near the apices of costules or costae may be only 0.1–0.2 mm long, flattened, and uniseriate. Away from the apices they become longer and pluricellular, with their transverse cell walls dark and somewhat conspicuous. Gradually, toward the proximal portions of the lamina they become two or more cells wide at the base, thus grading into scales. Detailed discussions are available in Moran (1986, 1987), who suggested they be called proscales, "since they are developmentally, and probably evolutionarily, precursors to scales." This contrasts with the "*Ctenitis*-hairs" (see key), which occur on the axes adaxially, maintain the same character throughout the lamina, and never grade into scales. Such proscales were observed in various species during treatment of *Ctenitis* for Guatemala and Peru but were of no apparent value as a diagnostic feature. Nevertheless, the character may turn out to be of much greater significance in the more detailed studies of a revision.

Veins

Thin vs. clavate vein tips is a major character in separating *Ctenitis* from *Megalastrum*. How-

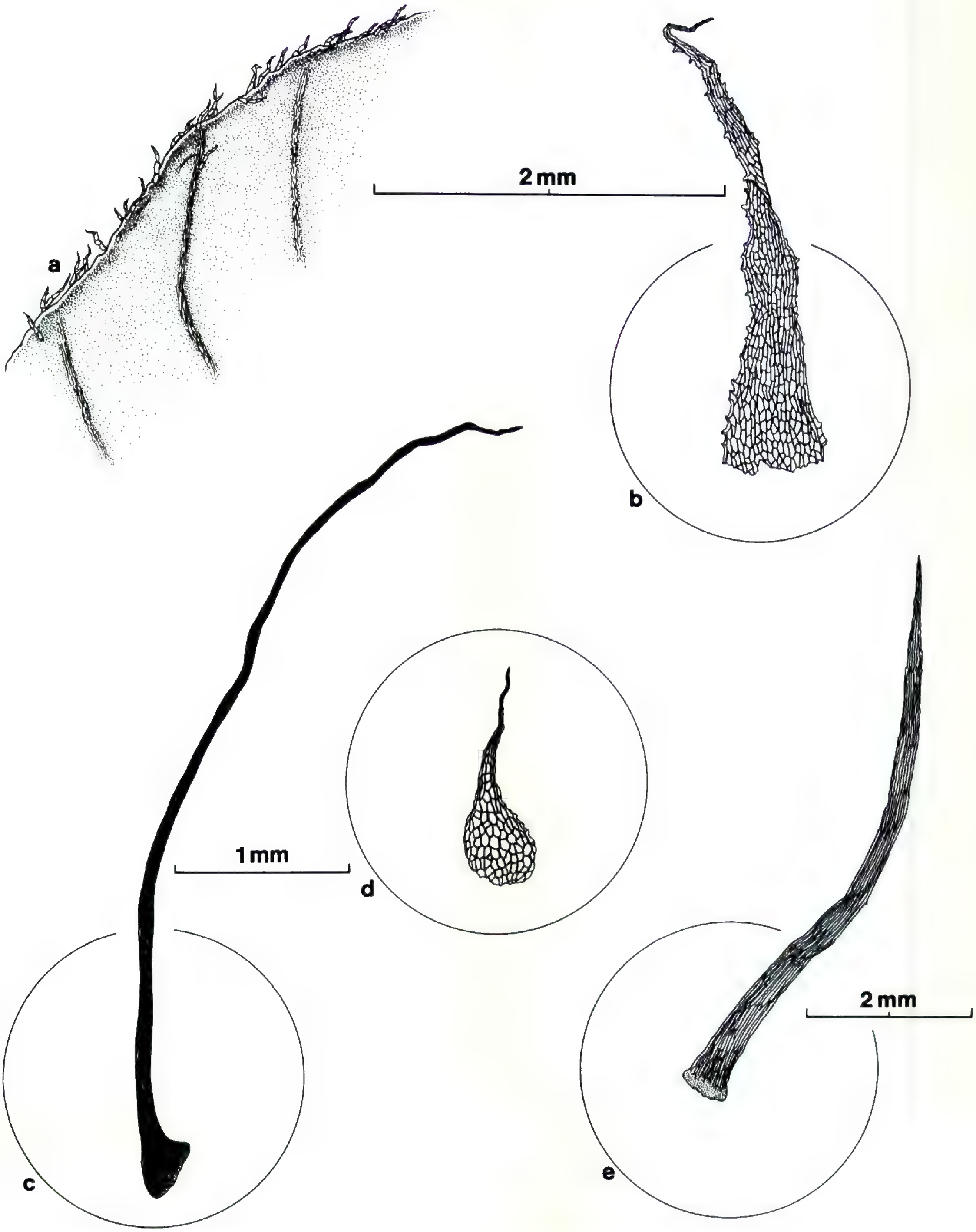

FIGURE 1. *Ctenitis* scales and trichomes. a, b. *Ctenitis microchlaena*—a. Segment margin, with trichomes (Peru, *Belshaw 3503*, F).—b. Rachis scale (Peru, *Belshaw 3503*, F).—c. *C. strigilosa*, petiole scale (Guatemala, *Standley 91874*, F).—d. *C. lanceolata*, costa scale (Guatemala, *Standley 91628)* .—e. *C. grisebachii*, petiole scale (Guatemala, *Steyermark 35102*, F).

ever, where the tips end in relation to the margin does not appear to be very important in distinction of species within *Ctenitis*. Between a few species there is some variation in the forking of veins from the segment midrib (simple vs. one-forked), as well as some difference in vein tip termination (nearly at the margin vs. well short of the margin). However, in neither my Guatemalan nor Peruvian stud-

ies have I found these features to be constant or greatly effective. *Ctenitis microchlaena* has basal veins of segments terminating at the margin well above the sinus, which helps separate it from *C. refulgens* and *C. submarginalis*, in which basal veins end short of the margin or reach it at or near the sinus. Compared with some other diagnostic features in the genus this is admittedly a subtle one. Nevertheless, I suggest it is worth more careful scrutiny in future research in *Ctenitis*.

Lamina

Most regional treatments of the genus have used the degree of dissection of lamina as an important key character. Least dissected laminae in *Ctenitis* are one-pinnate-pinnatifid, such as *C. refulgens*, *C. salvinii*, *C. submarginalis*, and *C. vellea* (Willd.) Proctor (Greater Antilles); whereas some of the larger-leaved species can be as much as four-pinnate-pinnatifid: *C. equestris* and *C. excelsa*. This separates species into artificial groups, since lamina dissection is intermediate in other species, varying from two- to three-pinnate-pinnatifid, and the dividing line can be shifted nearly anywhere an author wishes.

Many species of *Ctenitis* have enlarged, as well as more highly dissected, basal pinnae, such as *C. hemsleyana* (Hemsley) Copel., in which all except the basal pinnae are essentially one-pinnate-pinnatifid. Basal pinnae may be nearly three-pinnate, with basiscopic pinnules about the size and shape of adjacent pinnae. Consequently, caution should be used in writing and/or interpreting keys to such species. Furthermore, an herbarium specimen of a larger-leaved species can be misleading if it contains only the basal or apical portion of the lamina, without label data explaining the remainder of the lamina architecture.

Summary

All of the taxonomic characters discussed above may be variously effective in identifying the species of *Ctenitis* if the indicated cautions are heeded. However, groups may be artificial ones if separated by degree of lamina dissection, forking of veins, type of trichome, presence or absence of indusia, and soral position.

My studies of *Ctenitis* in Central and South America, appear to corroborate Christensen's theory that scale type is one of the best indicators of relationship. Regardless of lamina dissection or presence or lack of indusia, species with any of the following scale types probably have strongest affinity: (1) dark, filiform, with abruptly expanded base (Fig. 1c); (2) broad, flat, delicate, with fine cell walls and conspicuously clathrate (Fig. 1b); (3) broad, bullate, with attenuate tips (Fig. 1d); (4) linear, rigid, with thick cell walls, not or scarcely clathrate (Fig. 1e). Holttum (1985) believed that two natural groups of Old World species can be distinguished by their scales.

Several other characters might well be strong indicators of species affinity but need further comparison across the full range of distribution and should be assessed for degree of constancy: (1) basal veins of segments extending to near, or well above the sinus, and/or reaching or terminating short of the margin; (2) glands (color, shape, orientation) present or lacking on indusia or laminar surface; (3) segment margins with trichomes present or lacking; (4) spore morphology.

Since *Megalastrum* and *Triplophyllum* have been separated from Christensen's five original groups of *Ctenitis*, it is now necessary to determine if the remaining three constitute natural divisions. By far the largest of these is the *submarginalis* group, which was distinguished chiefly by simpler lamina architecture, i.e., leaves no more than one-pinnate-pinnatifid. However, this may be an artificial grouping, for too many of the species widely differ in the more significant characters mentioned above. The next largest group, *hirta*, contains species with three different scale types (1, 3, and 4 above), both ciliate and eciliate segment margins, and different types of glands. The smallest group, *ampla*, is distinctive at least in that its species all have type 2 scales. It thus appears that the latter may be the most natural group, and species complexes of the others should be examined to redetermine their proper relationships.

Among all the different scales, types 2 and 3 seem to be most closely related. Although the former is flat and the latter bullate, both are conspicuously clathrate with broad cells. The other two types have very small, or very narrow and crowded cells. Future studies should ascertain whether species of type 2 (*ampla*) and 3 (some species of *hirta*) share other significant features. Tryon & Tryon (1982) concluded that Christensen's *hirta* group had too many diverse characters and divided its species between the other two, principally supported by features of the spore surface. Therefore, it will be important to learn whether species with scale types 2 and 3 have the same kind of spore ornamentation. If so, this would effectively delimit two discrete species groups in the place of the three polymorphic groups earlier recognized by Christensen.

Conclusion

The last six decades have produced dramatic results in the understanding of species groups once gathered under the umbrella of "*Dryopteris*." With the impetus furnished by Christensen, such genera as *Ctenitis*, *Cyclodium*, *Lastreopsis*, *Megalastrum*, *Stigmatopteris*, *Thelypteris*, and *Triplophyllum* have been correctly set apart, and many of their species have been clearly delineated. Definition of *Ctenitis*, in turn, recently has been simplified by the separation of *Megalastrum* and *Triplophyllum*. Yet this important pantropical genus of ca. 80 species still needs major revision. Major diagnostic characters have been highlighted here, based on knowledge I have gained from the studies of the genus in two floristic treatments, which included a canvass of most of its neotropical species. These characters have been subjected to close analysis and evaluated for efficacy, and suggestions have been made for their future correlation. It is hoped that this information will help in floristic studies and facilitate monographic work on the species remaining in *Ctenitis*.

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Epilogue

Although I had been acquainted with Alice and Rolla Tryon earlier, it was not until 1970 that our relationship developed into friendship. I had come to Harvard to ask Rolla's advice in selecting a genus for monographic study, my briefcase laden with potentials. We discussed them, one after another, and dismissed them, one after another. Finally he suggested one I hadn't considered: "Bob, here's a small, neotropical genus that really needs work, of just the right size, scope, and difficulty; it would suit you perfectly!" Once I'd been convinced, had I known him then as I do now, I would have properly interpreted the twinkle in his eye to mean, "Aha! Another candidate to cooperate on tree-fern research!"

The genus was *Cnemidaria*, and my ultimate publication was to be but one of many prompted by Rolla on the tree-ferns, a group that had long fascinated him. He has been the catalyst for dozens of papers on the subject, from standpoints of morphology, anatomy, and cytology, to virtually every other botanical discipline. With these studies also has come controversy—students and experts disputing theories on the phylogeny or taxonomy of tree-ferns. And the result? Probably no group of ferns has received so much attention from so many workers in so many disciplines, this with plants that had previously been almost entirely ignored and scarcely understood.

My periodic visits to the Gray Herbarium also demonstrated the unusual warmth and selflessness in Rolla, the teacher. No matter how deeply immersed in his own work, whenever I entered his office with a question he promptly cleared a space on the desk, pushed back his chair, lit his pipe, and became immediately receptive to my problems. I've observed this countless times, with his visitors, students, volunteers—everyone. How he was able to give so much of himself to others and still publish scores of significant fern works is still a mystery.

This warmth, cooperation, and academic excellence was two-fold for the Gray Herbarium visitor. In the room adjacent to Rolla's quiet office was Alice Tryon's beehive of pteridological activity, where this dynamic, hustle-bustle, perpetual-motion lady held sway. In many visits to the Tryon offices I have few recollections of Alice sitting, but I know she must have, as she spent hours at the microscope and scanning electron microscope. Nevertheless, she, like Rolla, always had time to answer questions. She was a walking encyclopedia of information about fern spores and freely shared her knowledge with anyone. A number of times she pointed out to me spore characters that helped confirm or deny species relationships. Moreover, she was ever concerned with ferreting out and suggesting lunchtime or evening activities and excellent

restaurants in the Harvard area, all with the purpose of making guests feel welcome.

It is fortunate for pteridology that Rolla and Alice took time off from their individual projects to collaborate on their magnum opus, *Ferns and Allied Plants*. This massive and impressive work sums up the knowledge of all genera (and many species) of neotropical pteridophytes in a way accessible to all. Nothing quite like it has been produced in nearly half a century, and it stands as a synthesis of the Tryons' historic contributions to pteridology. They have unselfishly dedicated themselves to the study of a major group of organisms. Our science is much richer for their efforts; and for those of us fortunate enough to be numbered among their friends, our lives are much richer for their being here.

DEFENSE STRATEGIES IN BRACKEN, *PTERIDIUM AQUILINUM* (L.) KUHN

Gillian A. Cooper-Driver[1]

ABSTRACT

In 1877 Francis Darwin expressed his belief that the primary role of nectaries in bracken is as waste glands, and that ants associated with bracken nectaries play no role in defending the plant because bracken is enemy free. This paper provides evidence that, in fact, bracken supports a large number of pathogens and herbivores. Bracken synthesizes a wide variety of secondary metabolites, which act as toxins and deterrents to these natural enemies. While ants may have been significant in selecting for specialist insect communities on bracken, it is doubtful whether they play a protective role and improve bracken fitness. Although Francis Darwin was wrong in assuming that bracken has no natural enemies, over 100 years later the question of whether the ant–bracken association is mutualistic continues to intrigue us.

My first acquaintance with Alice and Rolla Tryon was a wonderful day we spent together at Down House in Down, Kent, approximately 20 miles south of London. It was here in Down House that Charles Darwin lived with his family from 1842 until his death in 1882. It was here that he wrote *The Origin of Species by Means of Natural Selection* and his papers on plants: "The Fertilization of Orchids"; "The Variation of Plants and Animals under Domestication"; "Insectivorous Plants"; "Climbing Plants"; "The Effects of Cross and Self Fertilization in the Vegetable Kingdom"; "Different forms of Flowers in Plants of the Same Species"; and "The Power of Movement of Plants" (Darwin, 1892). The last of these was jointly published with his third son, the botanist of the family, Francis Darwin (Rendle, 1925).

There are many ferns growing in the vicinity of Down House, including the ubiquitous bracken fern, *Pteridium aquilinum* (L.) Kuhn. Bracken was of particular interest to Charles Darwin and his son because it has extrasoral nectaries, which exude secretions attractive to ants (Fig. 1). In an appendix to a paper on glandular bodies in *Acacia sphaerocephala* and *Cecropia peltata*, Francis Darwin (1877) recorded his father's fascination with the nectaries: "Examined several ferns with *Myrmica* on them, and found the glands quite dry. Brushed off the ants, and in from 5 to 6 minutes distinct drops of secretion were formed." Especially interesting in this paper are Francis Darwin's own observations on the nectar glands of bracken and his views on their function.

Contrary to the then widely held opinion (Delpino, 1886–1889) that extrafloral nectaries serve as protection to a plant by attracting ants, which then ward off marauders, Francis Darwin believed that the primary role of bracken nectaries was as waste glands or excretory organs. As a result of his observations, he felt that bracken did not require protection by ants. He wrote, "This plant is singularly free from enemies not being eaten by the larger animals, by rodents or by grasshoppers" (F. Darwin, 1877).

This view expressed by Francis Darwin raises several interesting questions. Is it true that bracken has few natural enemies and therefore does not require the biotic protection of ants? Is the bracken–ant interaction mutualistic, i.e., do both partners benefit, the plants by increased protection against natural enemies and therefore by increased fitness, and the ants from feeding on the nectar secretions, which provide a rich source of sugars and amino acids? Or is this a commensalistic association, as Francis Darwin suggested, in which only the ants benefit, and the association results in no fitness benefit to the plant? If possession of nectaries does not confer a fitness advantage to the plant, why is this trait maintained?

Although research in the last 100 years refutes Francis Darwin's statements that bracken lacks natural enemies, the same controversy over the

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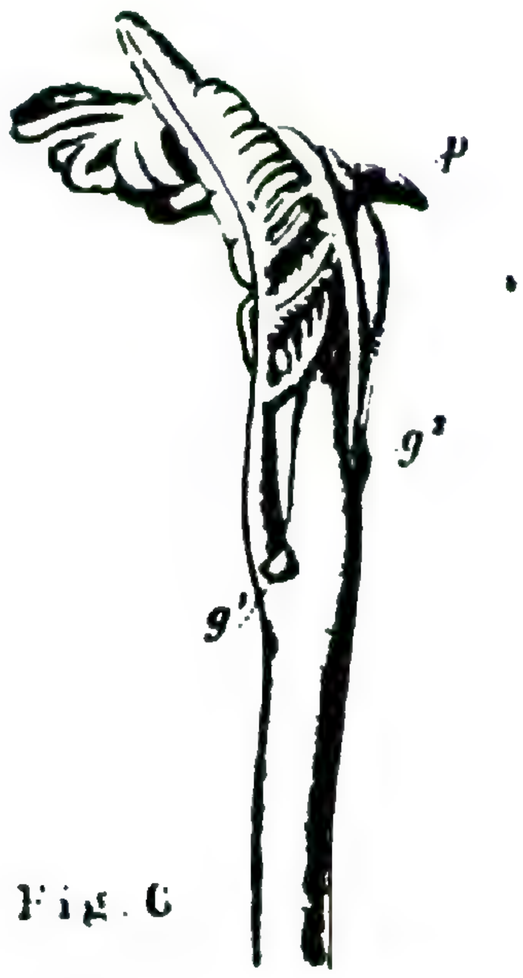

FIGURE 1. Fiddlehead of bracken showing the position of the nectaries (g^1, g^2). From J. Linn. Soc., Bot. Volume 15. 1877.

exact function of bracken nectaries continues as it did in Delpino's and Francis Darwin's time. This paper provides evidence that bracken does have natural enemies and considers why the role of nectaries in bracken appears to be so difficult to determine.

DOES BRACKEN HAVE NATURAL ENEMIES?

Bracken has always been a long-lived (Oinonen, 1967), aggressive, opportunistic weed (Page, 1976, 1982a), but probably because of increased deforestation bracken has spread extensively during this century, resulting in a severe loss of grazing land in many parts of the world (Page, 1982b). Even 60 years ago, bracken was described as "the ghost stalking silently at our side which nobody dares to discuss" (Tryon, 1941). Because bracken is so invasive, there is much interest in finding ways to eradicate it, particulary through developing methods for biological control (Perring & Gardiner, 1976; Dyer & Page, 1985; Kirkwood & Hinshalwood, 1985). This has resulted in an active search for the natural enemies of bracken, i.e., bracken pathogens, parasites, and herbivores.

Many species of fungi are known to be parasitic upon bracken (Gregor, 1932, 1938; Hutchinson, 1976; Webb & Lindow, 1981; San Francisco & Cooper-Driver, 1984; Bennell & Henderson, 1985), causing a range of different diseases. The most promising fungi in terms of biological control are three fungi that cause "curl-tip" disease in bracken. Combinations of *Phoma aquilina* Sacc. & Penz. (Coelomycetes), *Ascophyta pteridis* Bres. & Syd., and *Septoria* Sacc. have shown enough potential as biological control agents to be further investigated (Burge & Irvine, 1985; Burge et al., 1986).

Francis Darwin claimed that larger animals and rodents do not eat bracken. In fact, cattle, sheep, horses, deer (Braid, 1959), and humans (Hodge, 1973; L.A. Times, 1988) are now known to feed on bracken. Grazing by animals is one of the major concerns caused by the increased spread of bracken because feeding on bracken can often have drastic effects. Bracken can cause digestive tract and bladder tumors in humans, tumors and fatal hemorrhagic effects in sheep and cattle, and avitaminosis in pigs and horses (Evans, 1976; Taylor, 1989).

Francis Darwin's view that ferns, including bracken, are resistant to grasshoppers and other insect pests is not unique (Schneider, 1892; Brues, 1920; Erlich & Raven, 1964), but until recently there was little experimental evidence to support or refute this belief. During the 1970–1980s, many reports on phytophagous insects and arthropods colonizing ferns appeared in the literature showing that, in fact, ferns support a rich insect fauna (Balick et al., 1978; Hendrix, 1980; Ottosson & Anderson, 1983a). Balick et al. (1978) listed well over 100 species of arthropods associated with bracken fern.

Many of the insect species found feeding on bracken are bracken specialists (Lawton, 1976; Cooper-Driver, 1978). Common phytophagous insects discovered on bracken in Britain and North America include hymenopteran sawflies (*Strongylogaster*, *Aneugmenus*, and *Tenthredo*), lepidopteran larvae, e.g., species of *Callopstria* and *Papaiperma* (Noctuidae), dipterans that mine the stems and tips of the pinnules (*Chirosa* sp. (Agromyzidae)), and *Dasyneura* species (Cecidomyiidae), which induce galls. Sucking insects, such as *Macrosiphum* (Aphidae), are also common in the northern hemisphere (Lawton & MacGarvin, 1985).

Lawton has studied insects associated with bracken in North Yorkshire, England (Lawton, 1976, 1982; Lawton & MacGarvin, 1985), Hawaii, New Mexico, and Arizona, U.S.A., and Papua New Guinea (Lawton, 1982, 1984), and he has conducted preliminary surveys in South Africa, Australia, and New Zealand. As expected, these surveys have shown that the types of phytophagous insects found on bracken vary in each geographic area. Lawton has shortlisted two South African moths, *Conservula cinisigna* and *Panotima*, as possible biological control organisms.

Present evidence on bracken pathogens and herbivores, albeit regional and somewhat limited, cer-

tainly suggests the Francis Darwin was wrong in saying that bracken has no natural enemies.

Bracken has been described by Harper (1977) as one of the five most common plants in the world, suggesting a fair degree of ecological success. How then does bracken deal with its natural enemies, by chemical defenses and/or from protection by ants?

The Role of Chemistry

For a single plant species (Tryon & Tryon, 1982), bracken contains an unusually large and diverse number of secondary compounds (Cooper-Driver, 1976; Lawton, 1976; Jones, 1983; Ottosson & Anderson, 1983b). Compounds include sesquiterpene indanones (pterosides and pterosins); carcinogenic and mutagenic norsesquiterpene, ptaquiloside; the enzyme thiaminase, a vitamin B_1-decomposing enzyme; cyanogenic glycosides that release cyanide (Cooper-Driver & Swain, 1976; Schreiner et al., 1984); phytoecdysteroids or insect molting hormones; phenolic compounds, phenolic acids, flavonoids, and tannins (Tempel, 1981; Cooper-Driver, 1985); lignins; and silicates. Effects of phytochemical variation on colonization by insect communities has been reviewed by Jones (1983). Many of these compounds are toxic or deterrent and defend bracken against potential pathogens and predators, suggesting that chemistry must have played an important role in the ecological success of bracken.

Do other factors play a role in the protection of bracken from its natural enemies? Do ants provide an alternative defense strategy as they do in many other plants (Bentley, 1977; Beattie, 1985; McKey, 1988)?

The Role of the Nectaries

Relationships with ants are not uncommon in ferns as evidenced by the conspicuous stem modifications of ant-inhabiting ferns (Wagner, 1972; Gomez, 1974), and the morphological adaptations of fern spores for ant dispersal (Tryon, 1985). Nectaries occur in a number of fern genera in addition to bracken, namely *Polybotrya*, *Polypodium*, and *Drynaria* (Koptur et al., 1982), but the nectaries of bracken have been the most studied (Darwin, 1877; Figdor, 1891; Potonie, 1891; Lloyd, 1901; Luttge, 1961; Schremmer, 1970; Page, 1982c; Power & Skog, 1987).

Many different types of ants have been recorded as feeding on bracken nectaries (Lawton & Heads, 1984). Tryon (1941) wrote, "Large red and black ants were attracted by the exudation and observed in considerable numbers feeding upon them (the bracken nectaries)." Ants are not the only arthropod species that have been observed visiting the nectaries; parasitic wasps, coccinellid beetles, flies, and spiders also visit (Douglas, 1983; Tempel, 1983).

The assumption has always been that the association between ants and bracken nectaries is facultative; the ants are opportunistic feeders, drawn to a source of sugars and proteins. However, we know relatively little about the behavioral ecology of the ants that visit bracken nectaries, and perhaps this aspect should be further scrutinized.

Does the presence of ants provide protection for bracken? There are conflicting reports in the literature. Tempel (1983), studying ants on bracken in New Jersey, could find no evidence for ants playing a protective role. She did not observe any aggressive behavior by the ants, nor did she find that there was any difference in herbivore damage on control leaves, plants in which ants were present at the nectaries, as compared with on leaves from which ants had been excluded. Lawton & Heads (1984), in an extensive study of North Yorkshire and New Mexican bracken, reached the same conclusion. Field experiments designed to test the role of ants by excluding them from bracken leaves failed to produce convincing evidence that ants depress insect herbivore populations (Heads & Lawton, 1984). Further studies in South Africa (Rashbrook et al., 1989) also could not prove this.

However, there is evidence that in some cases ants do protect bracken. Douglas (1983), studying bracken in Michigan, noticed that different ant species behave differently toward herbivorous insects. Douglas observed that the larger ants, *Formica* and *Camponotus* species, defend the nectaries; any marauders are bitten, stung, or killed. Two smaller species of ants, *Tapinoma* and *Leptothorax*, apparently only feed and do not play a protective role. A survey of matched sites with and without wood ants (*Formica lugubris* Zett) revealed consistently lower populations of external feeders when wood ants were present (Heads, 1986). However, the only statistically significant differences between the insects at the experimental sites were for guilds of sucking insects. When foreign lepidopteran larvae of *Plodia* were experimentally placed on the leaves of bracken, the ants immediately removed them (Lawton & Heads, 1984).

Although in some cases ants obviously attack generalist phytophagous insects, what about the insects that normally feed on bracken, bracken

specialists? Lawton & Heads (1984) have shown that some of the most common specialist insect herbivores of bracken possess characteristics that make them immune to predation by ants. For example, bracken sawflies (*Strongylogaster*, *Aneugmenus*, and *Tenthredo*) have a distasteful, viscous hemolymph that repels ants (Pasteels et al., 1983; Heads & Lawton, 1985). Sawfly eggs are also apparently immune to ant attack. Other bracken specialists, such as gall formers and mining insects, feed inside the tissues and are inaccessible; others hide or jump away from patrolling ants. It appears that over periods of evolutionary time bracken insects have evolved and adapted to avoid ants (Heads & Lawton, 1984). Because the majority of insects found feeding on bracken are specialists, the generalist natural enemies of these herbivorous insects, i.e., the ants, may have provided the major selective pressure for restricted host–plant range (Bernays & Graham, 1988). Jeffries & Lawton (1984) also predicted that predators (in this case ants) are often potent selective agents and are likely to select for prey (insects) characteristics that reduce the impact of predators. The insect species thus evolves to occupy enemy-free space. The high proportion of specialist sawfly species, gall formers, and miners that make up the bracken herbivore community could therefore have been markedly influenced by ant predation.

Conclusion

Bracken defense and control still pose a number of evolutionary and ecological questions—for example, was the bracken–ant association once mutualistic? Unfortunately, we cannot always know what took place in the past. Are nectaries an example of a structure that was once useful but whose function is no longer obvious, just as phytoecdysteroids may have once acted as a defense against insects (Cooper-Driver, 1976), or are they examples of structures whose role is yet to come? The exact nature of the association is difficult to resolve until we know more about the ants and associated insects in different parts of the world. Almost all the detailed information we have comes from temperate areas, and we do not know what role ants associated with the nectaries play in defense in tropical regions. There is also still no conclusive evidence that ants improve the fitness of bracken.

Thus, it appears that Francis Darwin was probably right in believing that ants do not protect bracken, not because bracken does not have natural enemies, but because specialist bracken herbivores have evolved defensive mechanisms to deal with the ants.

Whenever I see ants at the nectaries of bracken I am reminded of the day at Down House and realize that in another 100 years bracken will still be around to puzzle and intrigue us. My heartfelt thanks go to the Tryons for introducing me to bracken and for stimulating a lifelong interest in the community ecology of ferns.

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PITYROGRAMMA CALOMELANOS (L.) LINK (ADIANTACEAE) ON LAYERS OF VOLCANIC ASH IN LOS TUXTLAS, STATE OF VERACRUZ, MEXICO

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Irma Reyes J.[1]

ABSTRACT

The selective establishment of *Pityrogramma calomelanos* (L.) Link on alternate layers of volcanic ash is described in this paper. The plants grow in layers of fine sand where the texture of the pyroclastic material and its moisture-holding capacity favors spore deposition and development of the plants.

Ferns tolerate diverse and extreme environmental conditions, particularly climatic and edaphic factors. There are very narrowly distributed species (e.g., *Adenoderris sororia* Maxon) while others have broad distributions (*Anogramma leptophylla* (L.) Link). The ranges are related primarily to dispersal and germination of the spores, and to the fitness of the species within various habitats. Fern species with wide ranges grow in ecologically open habitats where they frequently grow as pioneer species, experiencing low competition (Page, 1979b).

After release, the spores are exposed to physical factors such as gravity, wind, temperature, and humidity. With wind as the main dispersal agent, widespread dispersal to an array of differing habitats is possible. Fern spores can germinate at temperatures as low as 1–2°C or as high as 30–35°C (Miller, 1968), although the most favorable temperatures for germination of some species are 18–25°C (Pérez-García & Riba, 1982). High humidity helps reactivate the metabolism of the spore and promotes germination.

Spores germinate and prothallia usually grow on horizontal surfaces, but they can grow even on vertical slopes and on the roofs of caves (Page, 1979b). Since dispersal capability seems to be equivalent among homosporous ferns, establishment of the sporelings and plantlets must depend on ecological factors and fitness of the species in a particular niche (Tryon, 1972).

Ferns include species that invade disturbed habitats. *Pityrogramma calomelanos* is native and widely distributed in tropical America and has naturalized in the Old World. It is an effective disturbance colonizer throughout the tropics. This fern may have been introduced deliberately into the Old World as an ornamental plant or accidentally (Schelpe, 1975; Pérez-García et al., 1982).

Pityrogramma calomelanos has numerous features of a disturbance colonizer. It tolerates short dry periods (Tryon & Tryon, 1982), and it grows in open sites; it may be designated a heliophyte. Its spores have long viability, as is usual in non-chlorophyllous spores of homosporous ferns. The rhizomes resist such extreme conditions as high temperatures and high sulphur concentration at the substrate, as was shown by the plant regeneration after the 1982 eruption of the Volcán Chichonal in Chiapas, Mexico. Rapid regeneration under adverse conditions was evidenced by specimens with fertile leaves 1 m high, and abundant young sporophytes 5–7 cm high were found within 2 km of the crater of the volcano two years after the eruption (Spicer et al., 1985).

Here we describe the selective establishment of *Pityrogramma calomelanos* on a roadcut through successive strata of volcanic ash. The roadcut is located at km 106 of the Federal Highway 180, 14 km NW of Santiago Tuxtla, state of Veracruz, Mexico, at an altitude of 340 m. At this site, hills of Miocene volcanic ash have nearly horizontal alternating layers of different colors, textures, and compositions. The slope is strongly eroded, and almost vertical walls of ash are visible; the layers with ferns are clearly delimited (Figs. 1, 2).

The characteristics of the two kinds of strata are as follows: (a) layers of pale brown, fine ash

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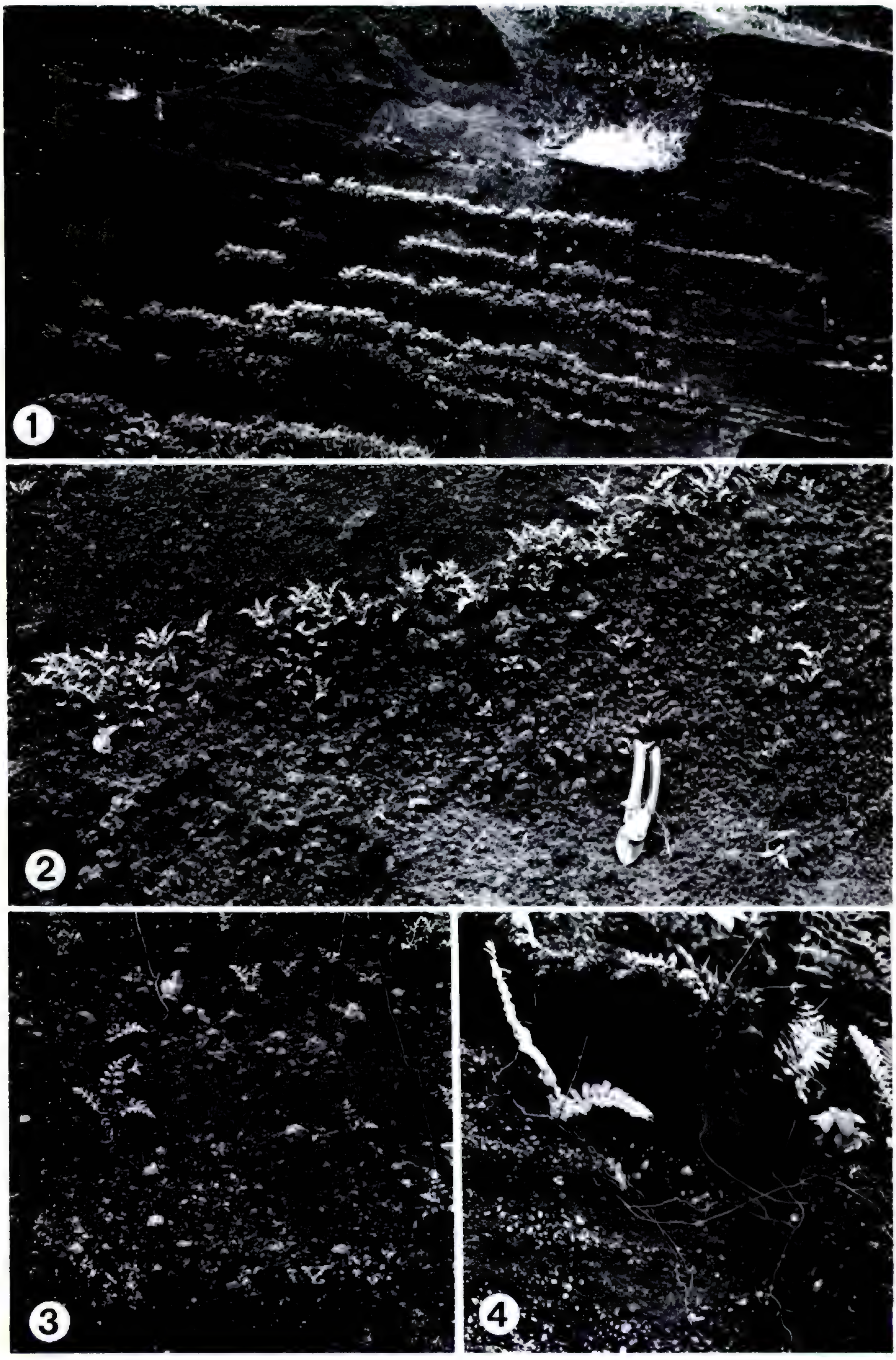
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1–10 cm thick with fine ash and basaltic tuffs predominating, moderate cohesiveness, and great absorption and retention of water; and (b) layers of gray ash, 1–50+ cm thick, made of coarser, noncohesive particles with basaltic gravel predominating.

Both layers react strongly to alophane (NaF and phenolphthalein), and they have weakly alkaline pH (7.5) in aqueous solution and slightly acidic pH (6.2–6.5) in saline solution (KCl 1 N pH 7). The qualitative analysis for soluble nutrients showed that the brown fine ash is richer in phosphorus and calcium than the gray coarse ash.

Pityrogramma calomelanos grows in the layers of fine ash, even where they are 1 cm thick. The species is restricted to specific layers, even where there is no soil in the strict sense, but regolite.

Why do these plants prefer the thin substrate of the fine ash to that of the coarse one, even when this is more abundant? While *Pityrogramma calomelanos* is considered a colonizer of well-drained substrates, in this case its restricted establishment in the thin layers of fine ash is affected by factors beyond drainage. The pH of the substrate is critical for establishment of some species, but *Pityrogramma calomelanos* can grow on rocks, slopes, river banks, and lava flows, and it has even been considered as a pumicicolous fern (Page, 1979a), colonizing well-drained volcanic habitats.

There are some studies about the edaphic preferences of ferns in which pH and calcium content of the substrate (Wherry, 1920; Hevly, 1963), kind of rock (Kruckeberg, 1964; Page, 1979a), pH, concentration of specific nutrients, percentage of humidity, the soil texture, and organic matter (Graves & Monk, 1982) are considered. Petersen (1985) assessed selected literature on edaphic adaptation of pteridophytes.

The results of the physical and chemical analysis of the two kinds of ash show that the preference for the fine ash is not determined by the pH nor by the chemical composition. The texture of the fine ash does favor aggregation and cohesiveness of the particles, which permits greater retention of water and nutrients than in the coarser substrate. The fine layer erodes more slowly than the gravel layers. These features facilitate establishment, and the rhizoids of the gametophytes attach easily to the aggregated particles of fine sand.

In the same roadcut there are ash walls that have not been disturbed recently. There other established liverworts, mosses, and lichens occur without selectivity; they cover both kinds of ash (Fig. 3). In those walls we find some individuals of *Nephrolepis cordifolia* (L.) Presl (Fig. 4) with long wiry roots. In the undisturbed roadcuts, decay products of bryophytes and other organic debris concentrate organic material, accumulate in the walls, and thus permit establishment of other vascular plants.

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Figures 1–4.—1. Ash walls showing ferns selectively distributed.—2. *Pityrogramma calomelanos* in layers of fine ash.—3. Ash walls with liverworts and mosses.—4. Ash walls showing *Nephrolepis cordifolia* with long wiry roots.

OBSERVATIONS ON THE REPRODUCTIVE BIOLOGY OF *ALSOPHILA* SPECIES AND HYBRIDS (CYATHEACEAE)[1]

David S. Conant[2]

ABSTRACT

The percent spore germination, prothallial gross morphology, and the structure of sex organs on gametophytes of *Alsophila* hybrids were compared with those of *Alsophila* species. The mean percent spore germination was lower in the hybrids than in species; however, germination rates as high as 43% were observed among the hybrids. Prothallial gross morphology was more variable in hybrids than in species. Many gametophytes of the hybrids, however, grew into normal, cordate prothallia that later became hermaphroditic. Detailed studies revealed no difference between the structure of sex organs of hybrids and those of species. Sperm and egg appeared to mature at about the same time indicating that species and hybrids have the potential for self-fertilization.

The Cyatheaceae are unique among the ferns because of the apparent lack of polyploidy (Tryon & Tryon, 1982) and the existence of fertile diploid hybrids (Conant, 1975, 1983; Conant & Cooper-Driver, 1980). The family is of further interest because it has been hypothesized that tree ferns form new species by a specialized form of diploid hybrid speciation called autogamous allohomoploidy (Conant & Cooper-Driver, 1980). This mode of speciation begins with the formation of a fertile diploid F_1 hybrid. At meiosis, this plant presumably produces genetically recombinant spores. If these spores grow into bisexual gametophytes, and if intragametophytic selfing occurs, a completely homozygous F_2 recombinant sporophyte would result. Its spores will be genetically identical, barring mutation and homoeologous chromosome pairing, and it could give rise to a colony of individuals that are recombinant for the morphological characters of the progenitor species. These plants would be morphologically distinct from the progenitor species. If selfing is the norm and outcrossing is rare, the colony would also be reproductively isolated from the parental types and would potentially constitute a new species.

Conant & Cooper-Driver (1980) presented two kinds of evidence that are consistent with this hypothesis. The first was the existence of five species of *Nephelea* (later treated as *Alsophila* by Conant, 1983) that recombined or blended unique morphological characters of sympatric or nearby species. The second was the occurrence of fertile diploid hybrids and morphologically recombinant hybrids in the mountains of Puerto Rico. Although spores of the hybrids were shown to germinate, the degree of hybrid fertility and the development of these spores into bisexual gametophytes capable of selfing was not documented.

The determination of whether the sex organs of hybrid gametophytes are functional can be made only in comparison to the gametangia on the gametophytes of species. A brief review of what is known about the prothallia of the Cyatheaceae will help to put our results into perspective. Stokey (1930) described the prothallia and sex organs of 14 species of Cyatheaceae, including three members of *Alsophila*. In general, antheridia do not appear on the prothallia of the tree ferns until they have formed a notch meristem and well-developed wings. There was no evidence of antheridia production at very early stages (5–25-celled), as is frequently found in polypodiaceous (sensu lato) gametophytes. Archegonia appear on the gametophyte after development of the cushion, which in the Cyatheaceae is always four or more cells thick. The mature archegonium has a neck, which is

[1] I thank two former Lyndon State College students for assistance with this project. Ms. Lynn Farrell helped in the spore germination study and Ms. Janice Rucker prepared the line drawings of gametophytes. Special thanks go to the late Professor Carl L. Wilson for help in embedding and sectioning the gametophytes, to Dr. David S. Barrington, Dr. Finley A. Bryan, and one anonymous reviewer for constructive criticism of the manuscript, and to Dr. Rod Zwick for assistance with the statistical analysis of the spore germination data. This research was supported in part by Advanced Study Grants from the Vermont State Colleges.

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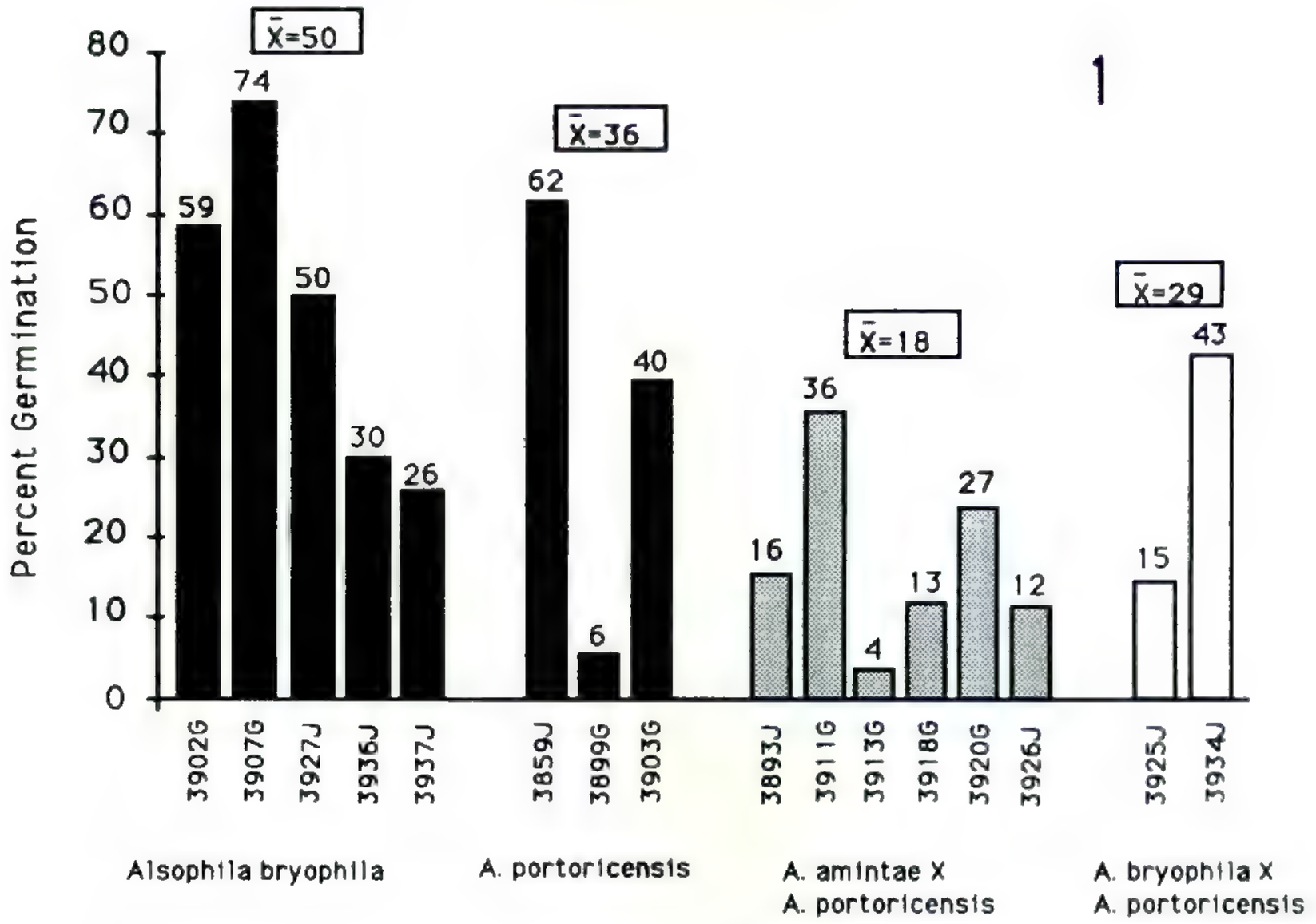


FIGURE 1. Comparison of percent spore germination of *Alsophila* species and hybrids. Numbers at tops of bars signify percent germination. Numbers in boxes indicate mean germination. Numbers below bars are collection numbers of Conant; J = Monte Jayuya, G = Monte Guilarte.

slightly curved toward the base of the gametophyte, the apical side of the neck usually being 6–7 cells, the basal side 5–6 cells. The ventral canal cell and the egg are situated directly below the neck canal nuclei. Occasionally, divisions of the venter cells (the cells surrounding the egg) were observed as the archegonium matured. Stokey (1918) described such divisions adjacent to eggs on gametophytes of *Trichipteris aspera* (L.) Tryon (as *Cyathea muricata* Willd.) and *Alsophila tussacii* (Desv.) Conant (as *Cyathea tussacii* Desv.) as apogamous developments; however, in no case were these structures reported to give rise to sporophytes.

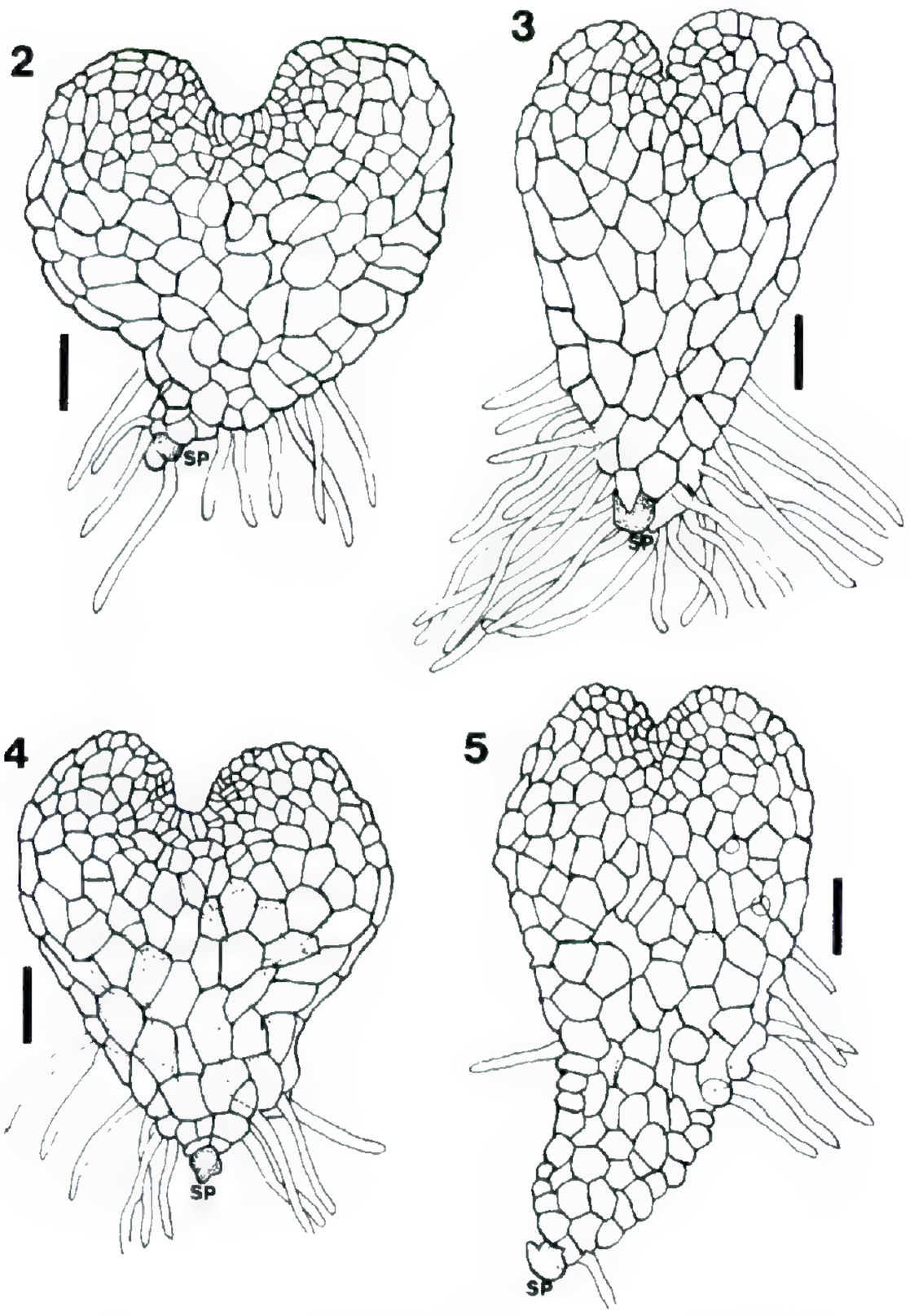
This paper compares the percent spore germination, prothallial gross morphology, and structure of sex organs of *Alsophila* hybrids with those of species in order to demonstrate the degree of hybrid fertility and to show that the hybrids have normally developed bisexual prothallia possessing the potential for intragametophytic selfing.

MATERIALS AND METHODS

Leaves of two *Alsophila* hybrids (*A. amintae* × *A. portoricensis* and *A. bryophila* × *A. portoricensis*) and two *Alsophila* species (*A. bryophila* and *A. portoricensis*) were collected on Monte Guilarte and on Monte Jayuya (ca. 10 km west and ca. 20 km east of Adjuntas, respectively) in the central mountains of Puerto Rico. Vouchers are cited in Figure 1 and are deposited at LSC. Spores were collected, sterilized, and sown in Puerto Rico according to the following protocol: fertile pinnules were washed under running water, blotted dry, and allowed to dehisce overnight in clean petri dishes. The following day, spores were surface sterilized with 1% sodium hypochlorite (commercial laundry bleach: Clorox), rinsed three times with sterile distilled water, and sown on sterile nutrient agar. These spore cultures were taped shut and transported back to the laboratory where they were kept in a growth chamber at 25°C for 12-hour days for three months. Percent germination was determined after six weeks by making three counts of 200 spores for different quadrants of each plate. The data was then subjected to the non-parametric Mann-Whitney test. Line drawings were prepared to compare the overall form of the gametophytes of hybrids with those of species. Gametophytes were grown to sexual maturity, and ten individuals of each hybrid and species were fixed in Randolph's Craf. The gametophytes were then dehydrated, embedded in paraffin, and sectioned serially at 10 microns. Sections were stained in safranin and fast green and mounted in Permount.

RESULTS AND DISCUSSION

The results of the spore germination experiments are shown in Figure 1. The Mann-Whitney test indicated a significant difference between the percent germination of *A. bryophila* and that of each of the hybrids. In *A. bryophila* the mean percent



FIGURES 2–5. Gametophytes of *Alsophila* species and hybrids.—2. *A. bryophila*.—3. *A. portoricensis*.—4. *A. amintae* × *A. portoricensis*.—5. *A. bryophila* × *A. portoricensis*. Dotted lines indicate regions where gametophytes were more than one cell thick. SP = spore from which gametophyte developed. All scale bars = 0.25 mm.

germination was 50% compared with 18% and 29% for *A. amintae* × *A. portoricensis* and *A. bryophila* × *A. portoricensis*, respectively. There was also a considerable range in the percent germination of species and hybrids, especially in *A. portoricensis* where germination varied from 6% to 62%. This large range rendered the percent germination data for *A. portoricensis* statistically indistinguishable from those of each of the hybrids even though the mean percent germination (36%) is higher for *A. portoricensis*. The lower mean percent germination in hybrids suggests that there is some spore inviability; however, spores appeared uniform in shape and size in all samples studied. The variation in percent germination among individuals of species and hybrids is probably a reflection of the maturity of the different spore samples when collected. None of the spore samples had 100% germination. This may be because the sterilization process killed a fraction of the spores in each sample. It should be noted that in a study of the germination of spores of four species of Cyatheaceae (Pérez-García & Riba, 1982), percent spore germination was temperature dependent. Cultures maintained at 25°C, however, had 100% germination. In contrast, among species of *Dryopteris*, germination ranged from 78% to 95%; however, one plant of *D. celsa* had only 37.3% germination indicating that the percentage of spores that germinate is not always high among individuals of a species (Whittier & Wagner, 1971).

Gametophytes of the species studied (Figs. 2, 3)

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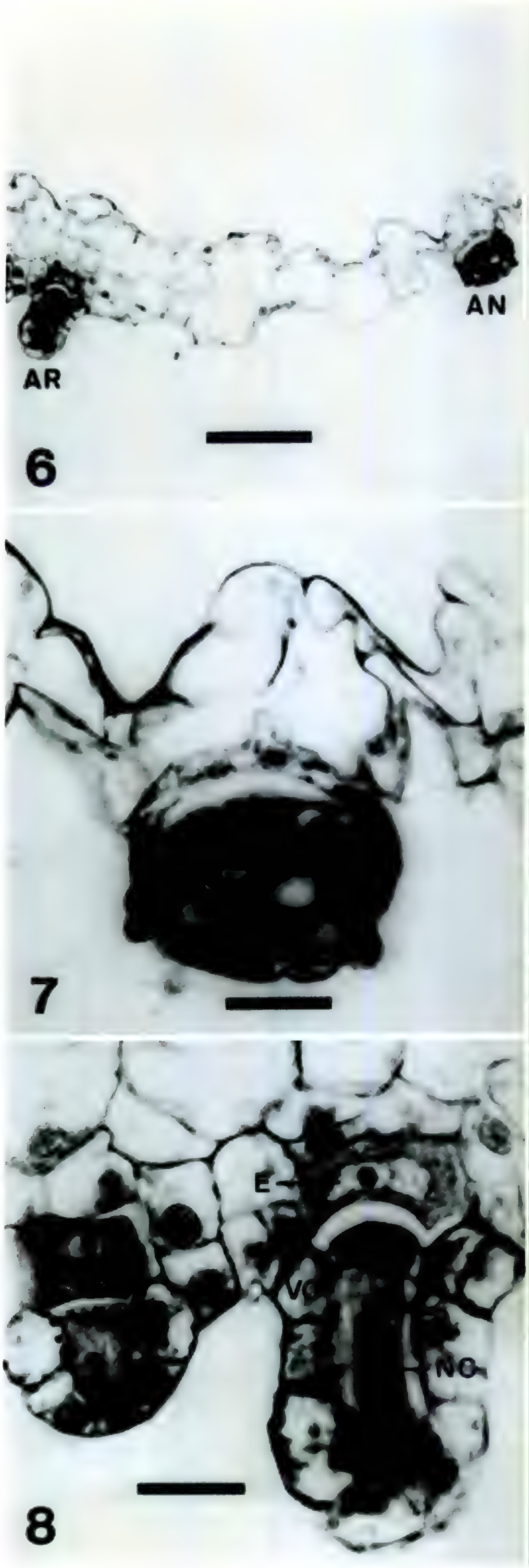
FIGURES 6–10. Gametangia of *Alsophila* species. 6–8. Micrographs from same section of *A. bryophila* gametophyte grown from spores taken from *Conant 4118*.—6. Bisexual thallus; scale bar = 0.1 mm.—7. Enlargement of antheridium shown in Figure 6; dark cells within are spermatids; scale bar = 0.025 mm.—8. Enlargement of archegonium shown in Figure 6: left, younger; right, mature; scale bar = 0.025 mm. 9, 10. Sections of different *A. portoricensis* gametophytes grown from spores from *Conant 4058*; scale bars = 0.025 mm.—9. Antheridium containing sperms.—10. Archegonia: left, nonmedial section; right, medial section, mature. Key: AN, antheridium; AR, archegonium; E, egg; VC, ventral canal cell; NC, neck canal cell.

FIGURES 11–16. Gametangia of *Alsophila* hybrids. 11–13. Micrographs from same section of *A. amintae* × *A. portoricensis* gametophyte grown from spores taken from *Conant 4104*.—11. Bisexual thallus; scale bar = 0.5 mm.—12. Enlargement of antheridium shown in Figure 11; coiled cells within are sperms; scale bar = 0.025 mm.—13. Enlargement of archegonium shown in Figure 11; near medial section; scale bar = 0.025 mm. 14–16. Same section of *A. bryophila* × *A. portoricensis* gametophyte grown from spores taken from *Conant 4106*.—14. Bisexual thallus, scale bar = 0.5 mm.—15. Enlargement of antheridium shown in Figure 14; dark cells within are spermatids; scale bar = 0.025 mm.—16. Enlargement of archegonium shown in Figure 14; nonmedial section, ventral canal cell indistinct; scale bar = 0.025 mm. See caption for Figures 6–10 for key to lettering on photographs.

FIGURES 17–20. Gametangia of *Alsophila* hybrids. 17, 18. Sections of different *A. amintae* × *A. portoricensis* gametophytes grown from spores taken from *Conant 4104*.—17. Antheridia containing sperms.—18. Archegonium, medial section. 19, 20. Sections of different *A. bryophila* × *A. portoricensis* gametophytes grown from spores taken from *Conant 4106*.—19. Antheridia containing sperms.—20. Archegonium, medial section. See caption for Figures 6–10 for key to lettering on photographs. All scale bars = 0.025 mm.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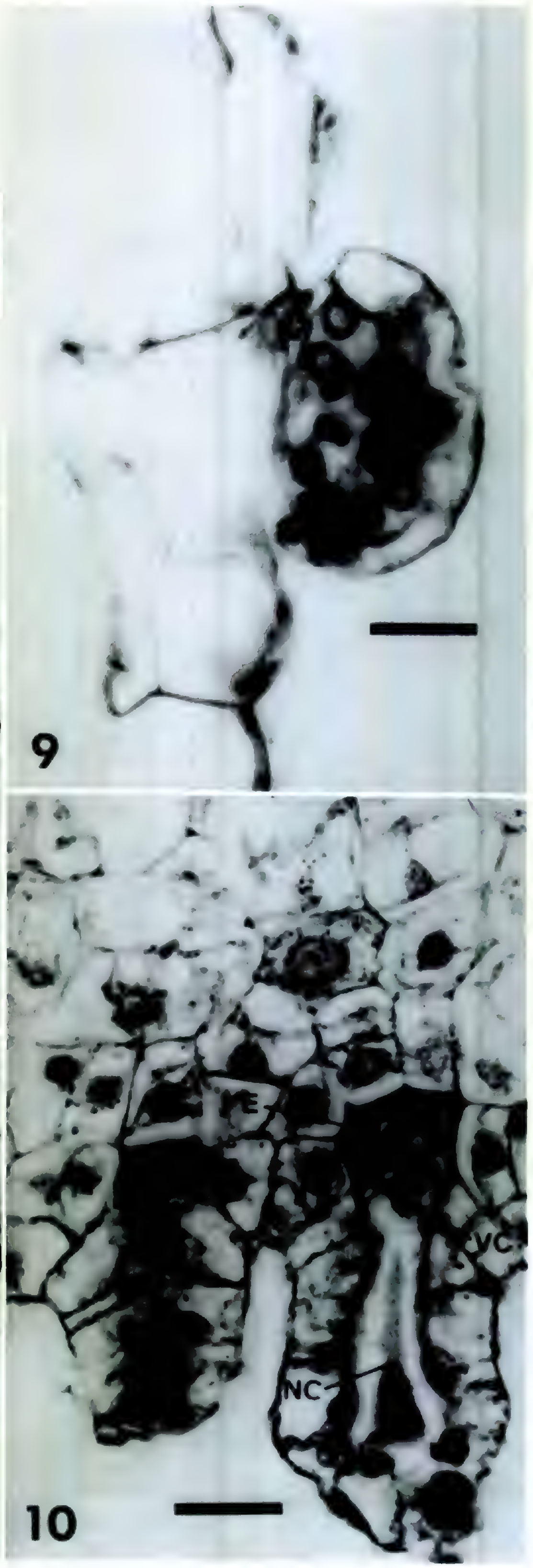
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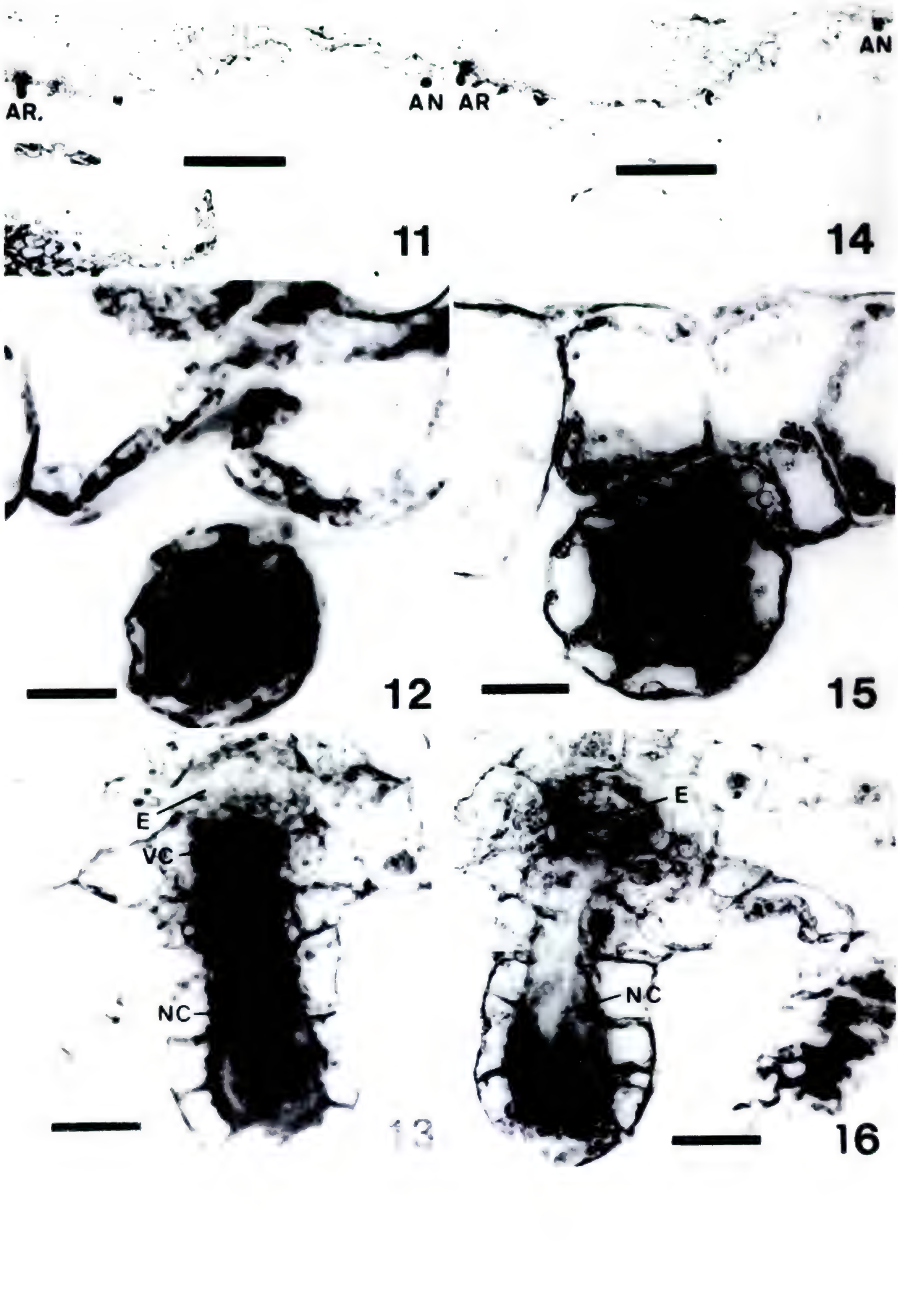
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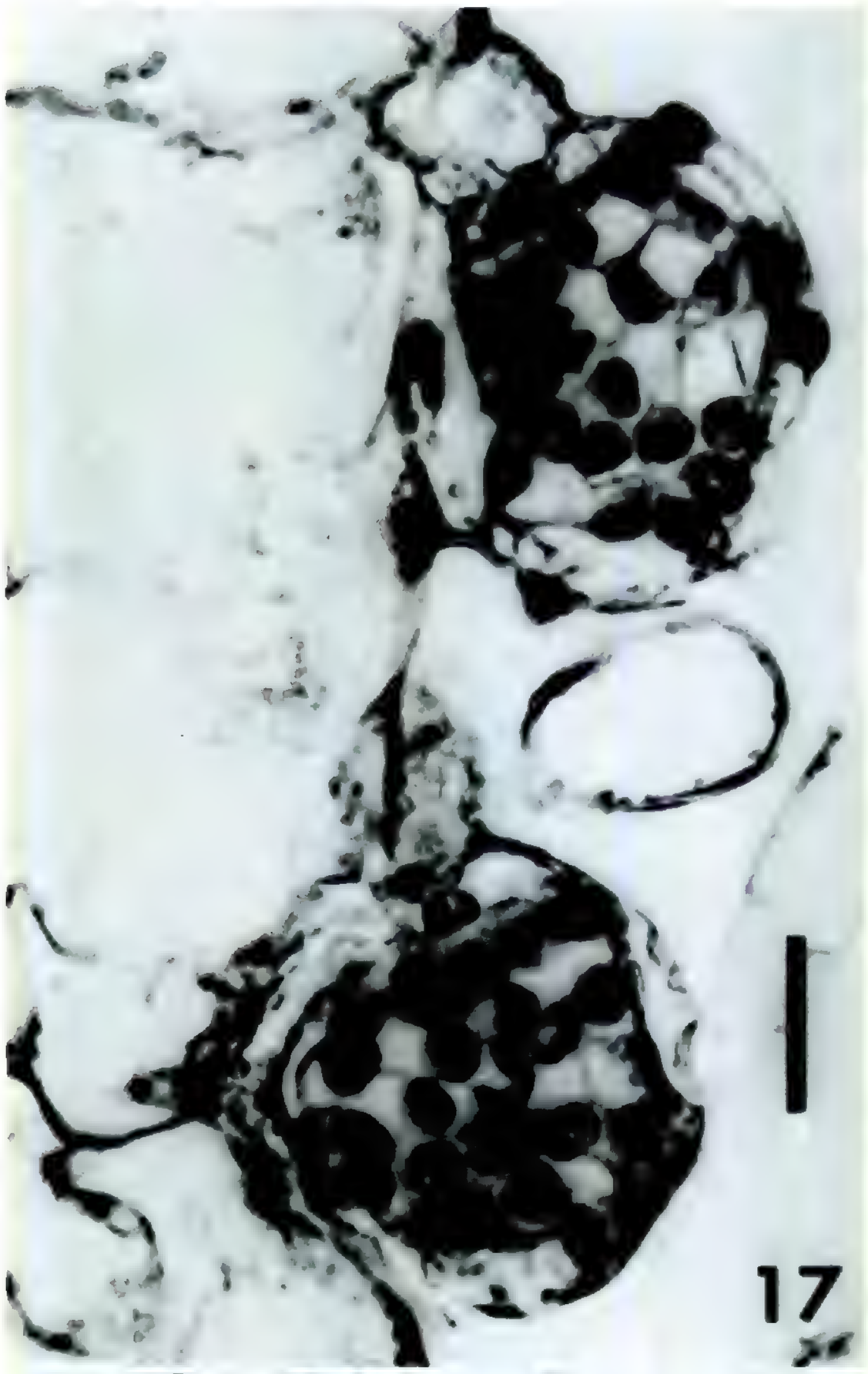
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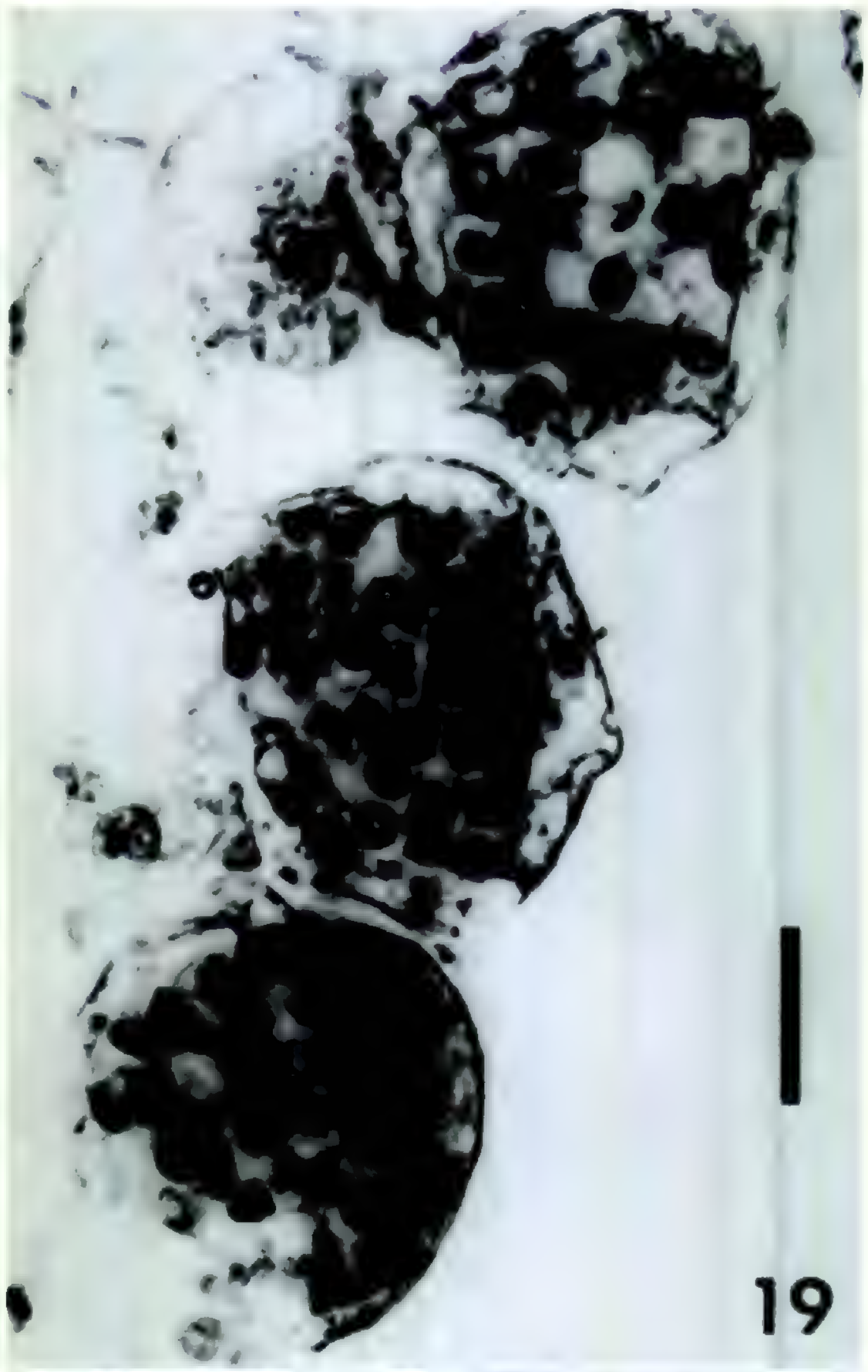
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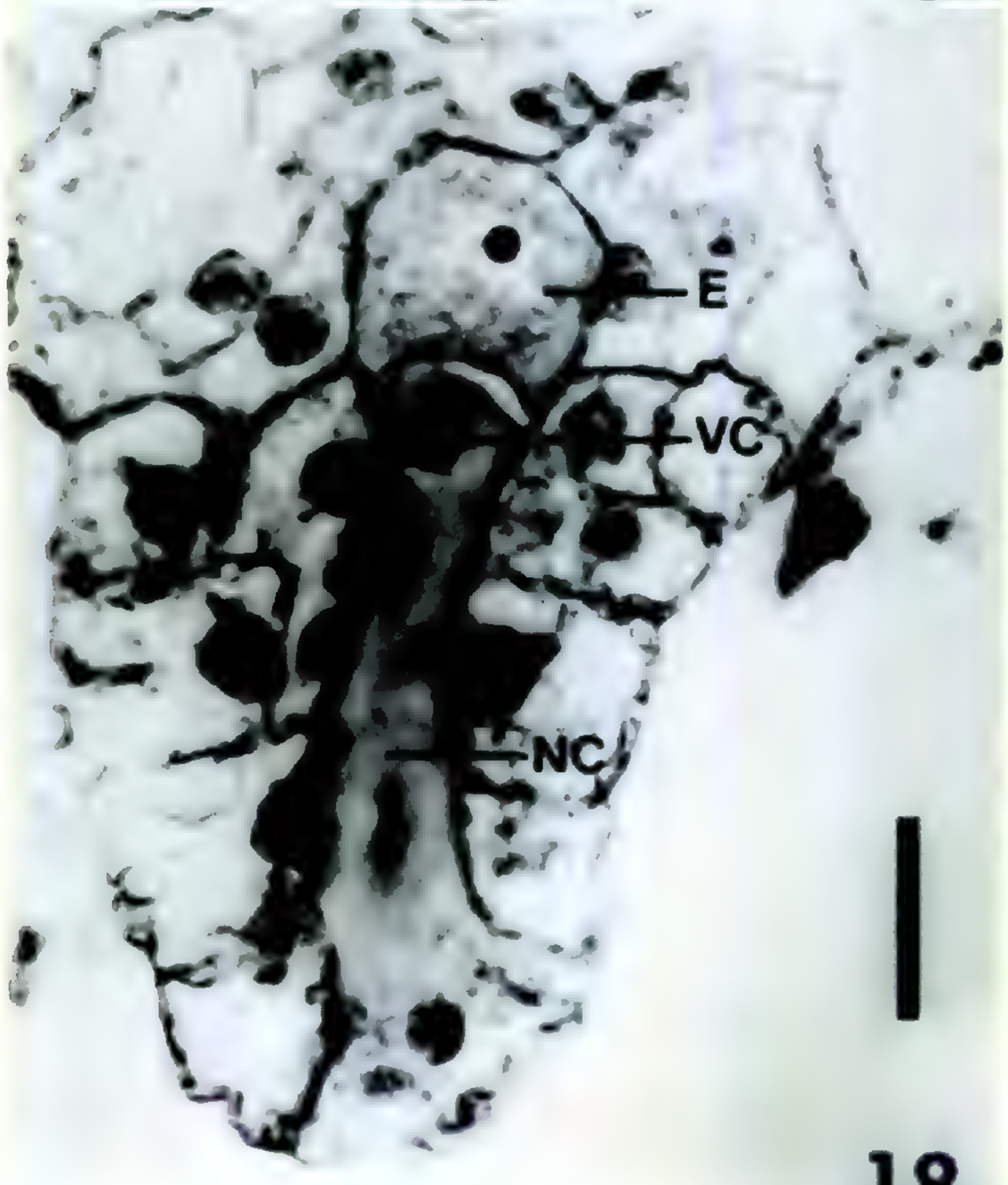
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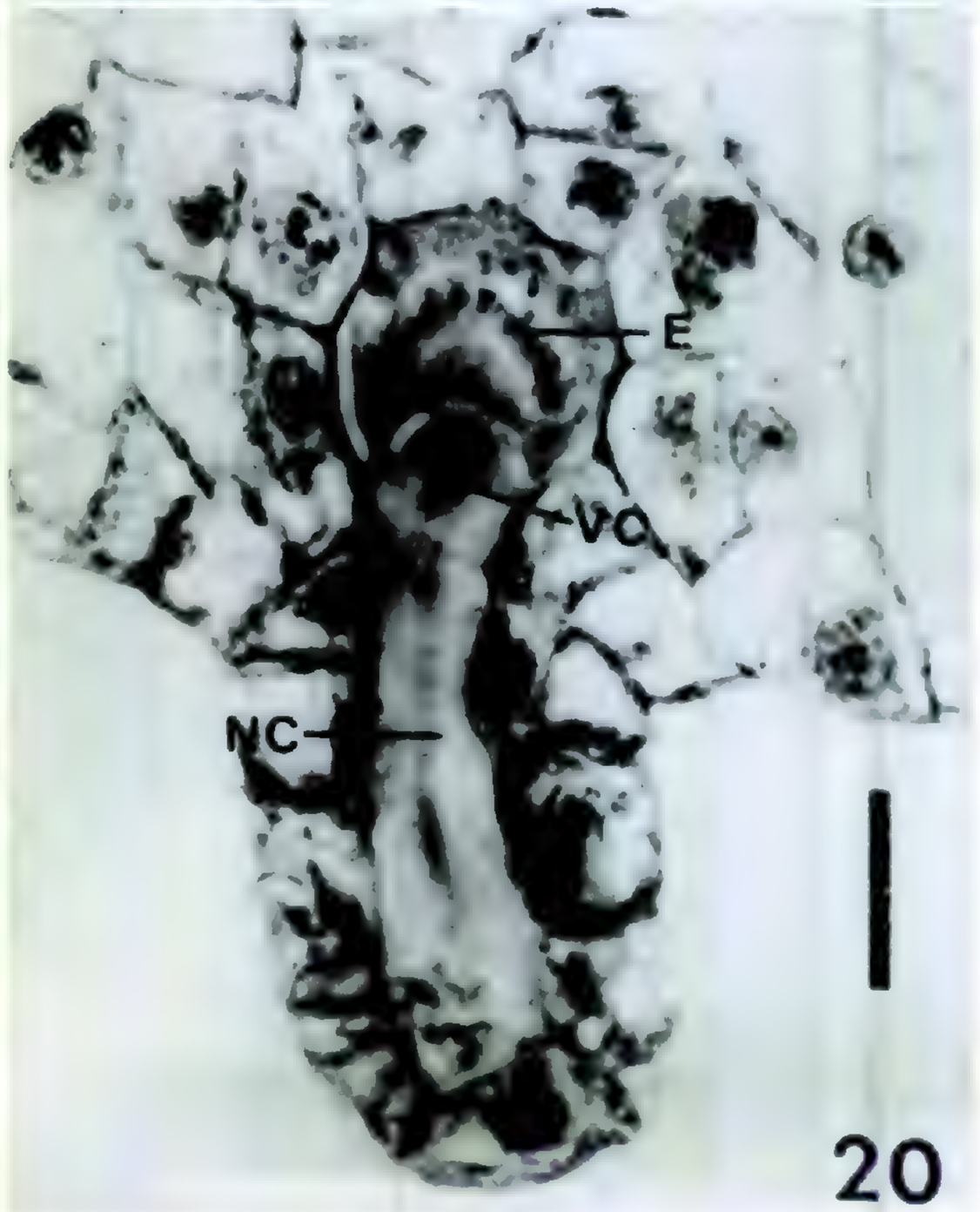
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grew into normal, cordate prothalli and were developmentally similar to those Stokey (1930) reported. Some hybrid gametophytes were smaller and appeared retarded in their development (not shown), although many grew into normal, cordate prothalli (Figs. 4, 5) and were closely similar to those of the species. The growth of these normal hybrid gametophytes appears to be free from the kinds of developmental abnormalities (Pray, 1971) that may be observed in gametophytes derived from the small percentage of viable spores often produced by "sterile" fern hybrids (Wagner et al., 1986; Whittier & Wagner, 1971).

Gametophytes of species and hybrids were sectioned serially to investigate their sexuality, to compare the structures of their gametangia and gametes, and to look for evidence of apogamous embryo formation. The gametophytes of all species and hybrids studied first produced antheridia. As a rule, antheridia were not formed until after gametophytes were beyond the stage of development shown in Figures 2–5. The gametophytes of species (Figs. 6–10) and hybrids (Figs. 11–16) became hermaphroditic after 2–3 months in culture. The gametangia and gametes of hybrids (Figs. 17–20) were similar in structure to those of the species observed in this study (Figs. 7–10) and to those described by Stokey (1930). Divisions of venter cells were observed in species and hybrids, although in no case did such divisions result in a mound of tissue resembling an apogamous outgrowth.

After three months of culture in the absence of water, no sporophytes had appeared. After this, the gametophyte cultures were maintained with occasional flooding for an additional six months. During this period, sporophytes appeared in cultures of both species and hybrids. It is presumed that these sporophytes arose as a result of normal sexual reproduction; however, whether these matings were the results of self- or of cross-fertilizations remains to be shown.

Gastony & Haufler (1976) documented well-developed archegonia on the apogamous triploid *Bommeria pedata* (Sw.) Fourn. After archegonia were mature, the egg degenerated and became necrotic. Sporophytes arose apogamously from vegetative cells peripheral to the archegonium. This apogamous life cycle included the Döpp-Manton type of sporogenesis, in which the chromosome number of spore mother cells is doubled prior to meiosis, resulting in the formation of diploid spores. Cytological examination of hybrid Cyatheaceae (Conant & Cooper-Driver, 1980; Conant, unpublished data) has demonstrated that the hybrids have an unaltered sporogenesis. The number of spore mother cells per sporangium (4) and the number of bivalents at diakinesis (N = 69) is the same in hybrids and species. Furthermore, necrotic eggs were not observed in the archegonia of the hybrids examined in this study. It therefore seems unlikely that the sporophytes appearing in cultures of hybrid gametophytes arose apogamously.

Although the mating system of tree ferns remains unknown, the bisexual condition and the synchronous maturation of male and female gametes indicate that the gametophytes of tree fern hybrids have the potential to self-fertilize. If this potential is realized in hybrid gametophytes, such as those shown here, and if the embryos and young sporophytes develop and grow normally, completely homozygous fertile F_2 hybrid sporophytes would result. If intragametophytic selfing is more common than outcrossing among gametophytes derived from these plants, it is possible that such homozygous hybrids would give rise to new, recombinant species. The mechanism that would maintain the reproductive isolation between these new allohomoploid species and their progenitors would be a mating system based on selfing.

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HYBRIDIZATION AND ALLOPOLYPLOIDY IN CENTRAL AMERICAN *POLYSTICHUM*: CYTOLOGICAL AND ISOZYME DOCUMENTATION[1]

David S. Barrington[2]

ABSTRACT

Cytological and isozyme data for four *Polystichum* species and four hybrids between them from the Sierra Talamanca of Costa Rica document hybridity and reveal a reticulate pattern of evolutionary relationships. Tetraploid *P. talamancanum* is hybridizing with tetraploid *P. orbiculatum* and with two diploid species, *P. speciosissimum* and *P. concinnum*, which also hybridize with each other. Cytological and isozyme data confirm that *P. concinnum* is one of two diploid progenitors of the allopolyploid *P. talamancanum*. *Polystichum talamancanum* and *P. orbiculatum*, also an allopolyploid, share an unidentified diploid progenitor. Homoeologous pairing demonstrated earlier in north temperate *Polystichum* hybrids was documented for these montane tropical hybrids. The demonstrated pattern of reticulation is similar to such patterns in ferns of north temperate regions.

The origin of fern species from sterile hybrids via chromosomal nondisjunction and polyploidization is supported almost entirely by work in north temperate regions (Manton, 1950; Lovis, 1977; Barrington et al., 1989). Studies in north temperate *Polystichum* (Dryopteridaceae) have played a critical role in demonstrating the contribution of hybridization and polyploidy to fern evolution (e.g., Daigobo, 1972; W. Wagner, 1973; Vida & Reichstein, 1975; D. Wagner, 1979; Barrington, 1986; Soltis et al., 1987). Recently, a similar pattern of reticulate relationships among fern species has been proposed for *Polystichum* in the Sierra Talamanca of Costa Rica and Panama (Barrington, 1985a, b, c; Barrington et al., 1986; Barrington, 1989; Barrington et al., 1989). In this paper, I use chromosome and isozyme data to document the proposed relationships and provide insights into hybridization and hybrid speciation of *Polystichum* in montane tropical regions.

Four *Polystichum* species are involved in hybridization in the Sierra Talamanca (Fig. 1). They comprise two broad-leafed diploid species, *P. concinnum* Lell. ex Barr. and *P. speciosissimum* (Kunze) R. Tryon & A. Tryon, and two narrow-leafed tetraploid species, *P. talamancanum* Barr. and *P. orbiculatum* (Desv.) Gay (Barrington, 1985a, b; Barrington, 1989). The forest-dwelling *P. concinnum* is endemic to the Sierra Talamanca, as is the low-alpine *P. talamancanum*. In contrast, the high-alpine *P. speciosissimum* is known from Mexico and Guatemala as well as Costa Rica, and *P. orbiculatum* is common in the high-alpine from Mexico to Bolivia.

Four hybrids between these species have been proposed (Fig. 1). Hypotheses for hybridity and hybrid parentage as well as definitions of species were based on morphological characters and degree of spore abortion (Barrington, 1989). Morphologically, the hybrids are noteworthy in that they include combinations of both morphologically disparate species such as *Polystichum concinnum* and *P. speciosissimum* and morphologically similar species such as *P. orbiculatum* and *P. talaman-*

[1] Rolla Tryon originally suggested that *Polystichum* in the American tropics was in need of systematic study. I thank Luis Diego Gómez P. for his support of my fieldwork in the Sierra Talamanca. Steven R. Hill, Peter T. Hope, Bruce Howlett, and Peter Zika all provided assistance in the field. Cathy Paris provided valuable insights in the laboratory and careful readings of the manuscript. David S. Conant also provided a critical review. An anonymous reviewer provided extensive, valuable suggestions that substantially improved this work. Electrophoretic and cytological work reported here was begun at the University of Kansas during the spring of 1985, when I spent a sabbatical leave in C. H. Haufler's lab. I thank Dr. Haufler for training in isozyme electrophoresis. The University of Vermont provided support for laboratory and fieldwork through its Institutional Grants BRSG-79 and BSCI85-1; this contribution was the specific goal of the latter grant.

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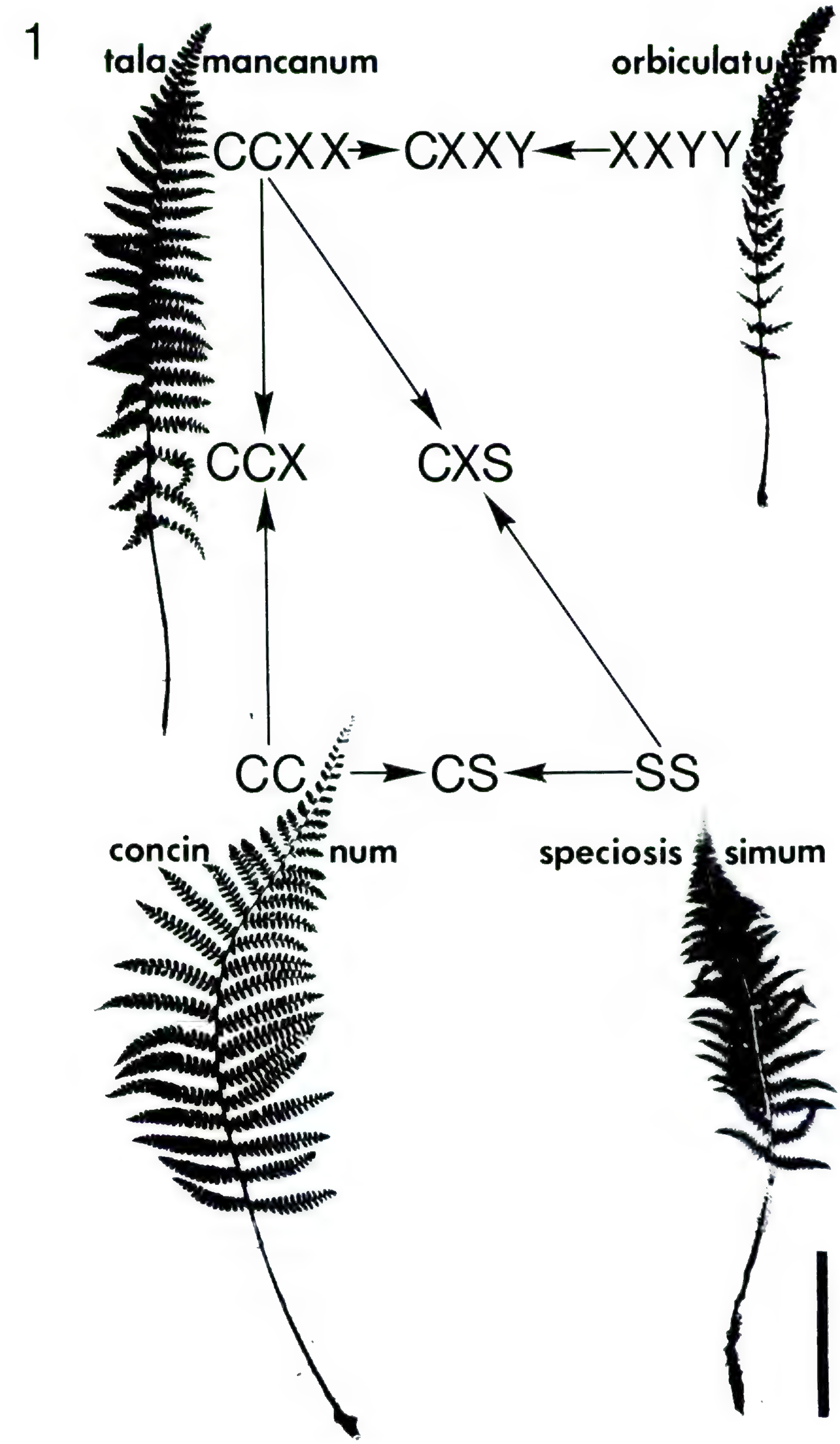
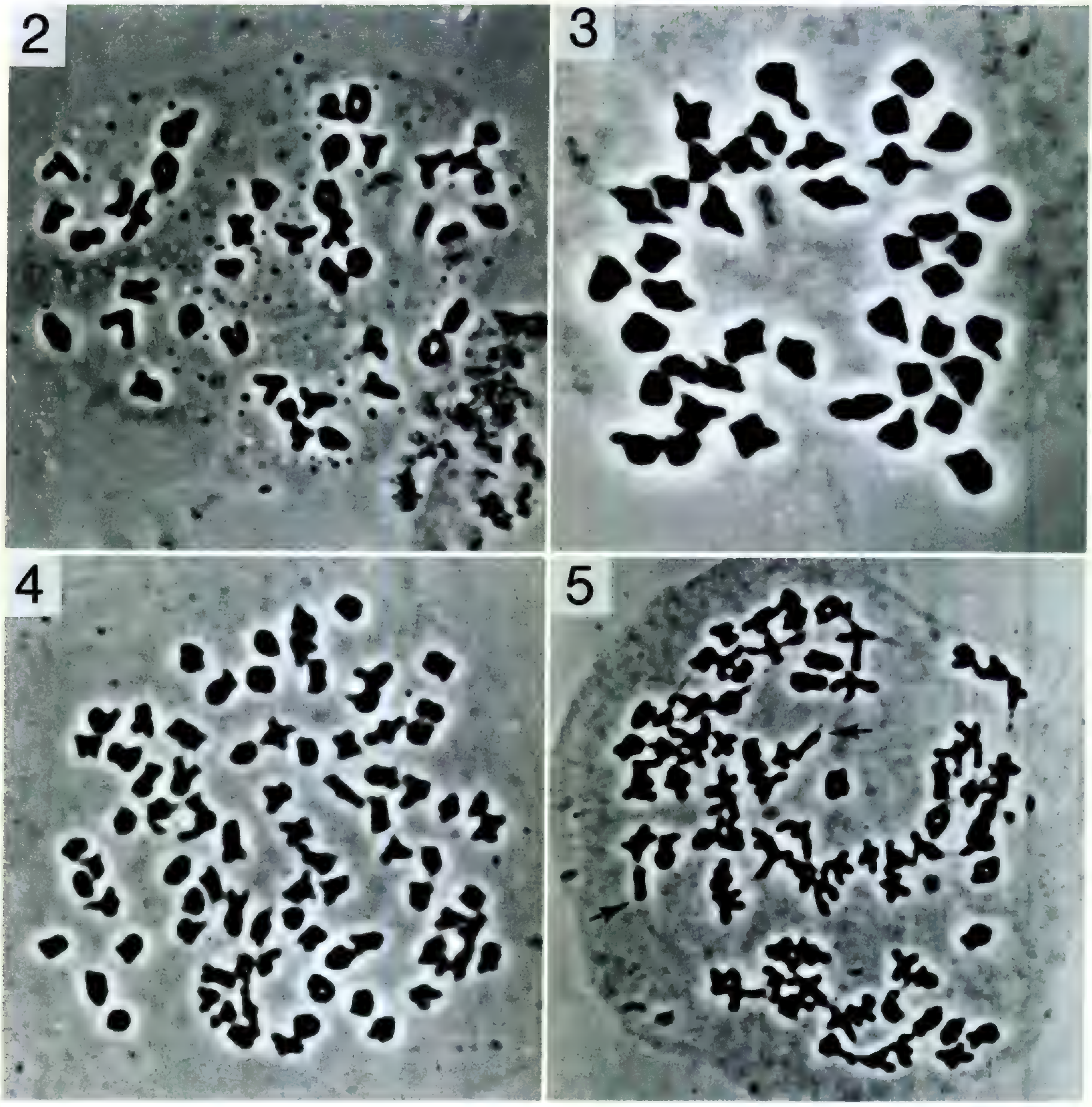


FIGURE 1. Proposed relationships between species and hybrids of *Polystichum* at Cerro de la Muerte, Sierra Talamanca, Costa Rica. Genomes are as follows: C: *P. concinnum*; S: *P. speciosissimum*; X: genome of undetermined derivation shared only by *P. orbiculatum* and *P. talamancanum*; Y: genome of undetermined derivation unique to *P. orbiculatum*. Collection numbers for greenhouse-grown leaves of species (all Barrington collections deposited at VT): *P. concinnum, 816*; *P. orbiculatum, 1273*; *P. speciosissimum, 1700*; *P. talamancanum, 1252*. Scale bar, lower right, is 15 cm.



FIGURES 2–5. Meiosis I of *Polystichum* species from Costa Rica.—2. *P. concinnum*, 41 pairs (*Barrington 822* VT).—3. *P. speciosissimum*, 41 pairs (*Barrington 976* VT).—4. *P. talamancanum*, 82 pairs (*Barrington 1261* VT).—5. *P. orbiculatum*, 81 pairs and 2 univalents indicated with arrows (*Barrington 1273* VT).

canum. The hybrids between closely allied species of *Polystichum* are especially difficult to distinguish morphologically because of overlap in ontogenetic and environmentally induced variation (Barrington, 1985a). A combination of morphological, cytological, and isozyme data is necessary to establish evolutionary relationships among these *Polystichum* taxa.

METHODS

FIELDWORK

Species and hybrids of *Polystichum* were collected during several trips to the Cerro de la Muerte, San José and Cartago provinces, Costa Rica, between 1980 and 1989. The study set comes from the montane rainforest and subalpine rain páramo at altitudes between 2,800 and 3,400 m; details of habitat and altitude for species and hybrids have been reported elsewhere (Barrington, 1985a, b, 1989).

CYTOLOGY

Field-collected species and hybrids for cytological work were cultivated at the University of Vermont greenhouses. Young sporangia for study of meiotic chromosome number and pairing were fixed in freshly mixed Farmer's solution (3 : 1 absolute ethanol : glacial acetic acid) for 18–24 hours, rinsed in 70% ethanol, and stored in 70% ethanol at 0°C.

TABLE 1. Fixed and common allozyme bands characteristic of Costa Rican *Polystichum* species. Both bands of fixed heterozygotes reported. Bands are reported as percent of fastest migrating band. Bands diagnostic of proposed diploid genomes labeled: C = *concinnum*, S = *speciosissimum*, X = genome of unknown origin shared by *talamancanum* and *orbiculatum*, Y = genome of unknown origin unique to *orbiculatum*.

	IDH		PGI-2		SkDH		TPI-1	
concinnum	82		100	C	100	C	68	
speciosissimum	100	S	83	S	84		68	
talamancanum	82		100	C	100	C	68	
			63	X	70	X		
orbiculatum	82		74	Y	84		86	Y
			63	X	70	X	68	

Material thus treated remained useful for analysis for at least three years. Staining of crushed sporangia was in 2% ferric acetocarmine at room temperature for about five minutes; Hoyer's solution was thoroughly mixed into the staining mixture before squashing.

ISOZYME ELECTROPHORESIS

To document the heritage of hybrids, fresh leaf samples from greenhouse-grown species and hybrids were ground in the phosphate extraction buffer of Haufler (1985) in preparation for electrophoresis on 12% starch gels. Electrophoretic procedures and staining schedules are as reported in Soltis et al. (1983). Triosephosphate isomerase (TPI), phosphoglucomutase (PGM), and phosphoglucose isomerase (PGI) were resolved on buffer system 6 of Soltis et al. (1983). Leucine aminopeptidase (LAP), aspartate aminotransferase (AAT), and hexokinase (HK) were assayed using buffer system 8 of Haufler (1985). System 11 of Haufler (1985) was used to resolve fructose 1-6 diphosphatase (F16DP), shikimate dehydrogenase (SkDH), isocitrate dehydrogenase (IDH), and malate dehydrogenase (MDH). All isozymes migrated anodally; isozymes were numbered from most anodal to nearest the origin. Allozymes are reported as percent of fastest-migrating band.

RESULTS

CHROMOSOME NUMBERS OF SPECIES

Here I provide chromosome numbers for each of the four species as a basis for inferences about parentage of the hybrids encountered. The counts are all first records for the species. On the basis of counts for nine individuals, *P. concinnum* is diploid with 41 pairs of chromosomes at meiosis I (Fig. 2). *Polystichum speciosissimum* is also diploid, with 41 pairs in meiosis I, based on several counts of a single individual (Fig. 3). *Polystichum talamancanum* is tetraploid, since it showed 82 pairs of chromosomes in meiosis I, based on a sample of five individuals (Fig. 4). Material from two sporophytes of *P. orbiculatum* collected on Cerro de la Muerte yielded counts of 82 pairs or 81 pairs and two univalents (Fig. 5), documenting it as tetraploid.

ISOZYME PATTERNS OF THE SPECIES

Unique combinations of fixed (or in one case very common) bands characterize the four *Polystichum* species from the Cerro de la Muerte (Table 1, Figs. 12–15). Two bands are diagnostic of *P. concinnum*: SkDH^{100} (present in all 14 sporophytes sampled) and PGI-2^{100} (present in 13 of 14 sporophytes sampled). *Polystichum speciosissimum* also has two diagnostic bands: IDH-2^{100} and PGI-2^{83}, both fixed in a sample of nine sporophytes. PGI-2^{100} and SkDH^{100}, shared with *P. concinnum*, were present in 25 sampled plants of *P. talamancanum*; the other alleles at each of these two loci (PGI-2^{63} and SkDH^{70}) have so far not been seen in diploid *Polystichum* species from Costa Rica. PGI-2^{63} and SkDH^{70}, fixed in *P. talamancanum* but absent in *P. concinnum*, were also present in all seven sampled sporophytes of *P. orbiculatum*. Two bands at fixed heterozygous loci, PGI-2^{74} and TPI-1^{86}, were unique to *P. orbiculatum* among Costa Rican species.

→

FIGURES 6–11. Meiosis I of *Polystichum* hybrids from Costa Rica.—6. *P. concinnum* × *P. speciosissimum*, 32 pairs and 18 univalents (*Barrington 1274* VT).—7. *P. concinnum* × *P. speciosissimum*, 40 pairs and 2 univalents (*Barrington 1274* VT).—8. *P. concinnum* × *P. speciosissimum*, 2 trivalents (indicated with arrows), 34 pairs, and 8 univalents (*Barrington 1274* VT).—9. *Polystichum concinnum* × *P. talamancanum*, 41 pairs and 41 univalents (*Barrington 1278* VT).—10. *Polystichum speciosissimum* × *P. talamancanum*, 31 pairs and 60 univalents (*Barrington 973* VT). 11. *Polystichum orbiculatum* × *P. talamancanum*, 51 pairs and 62 univalents (*Barrington 1283* GH, VT).

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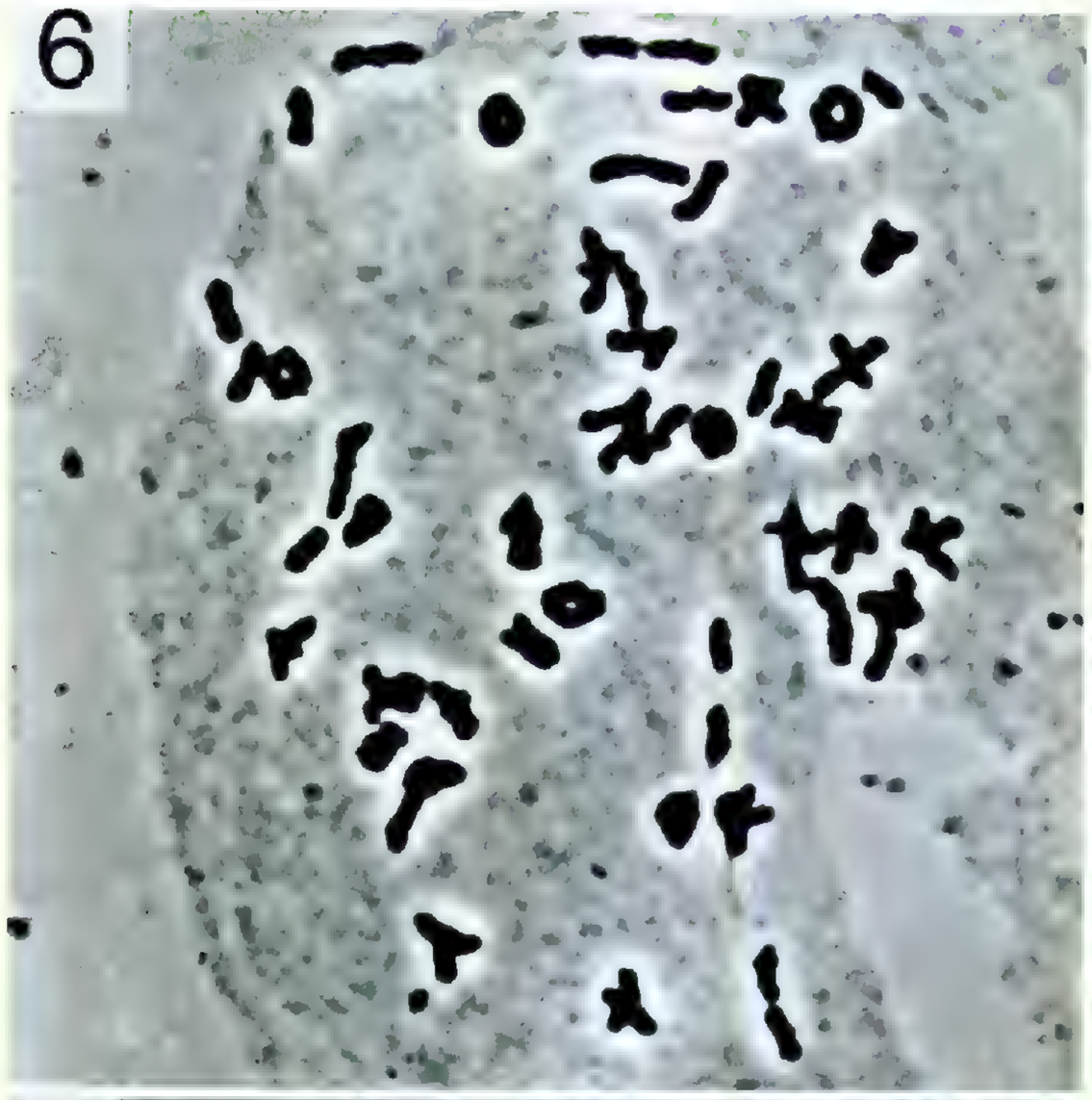

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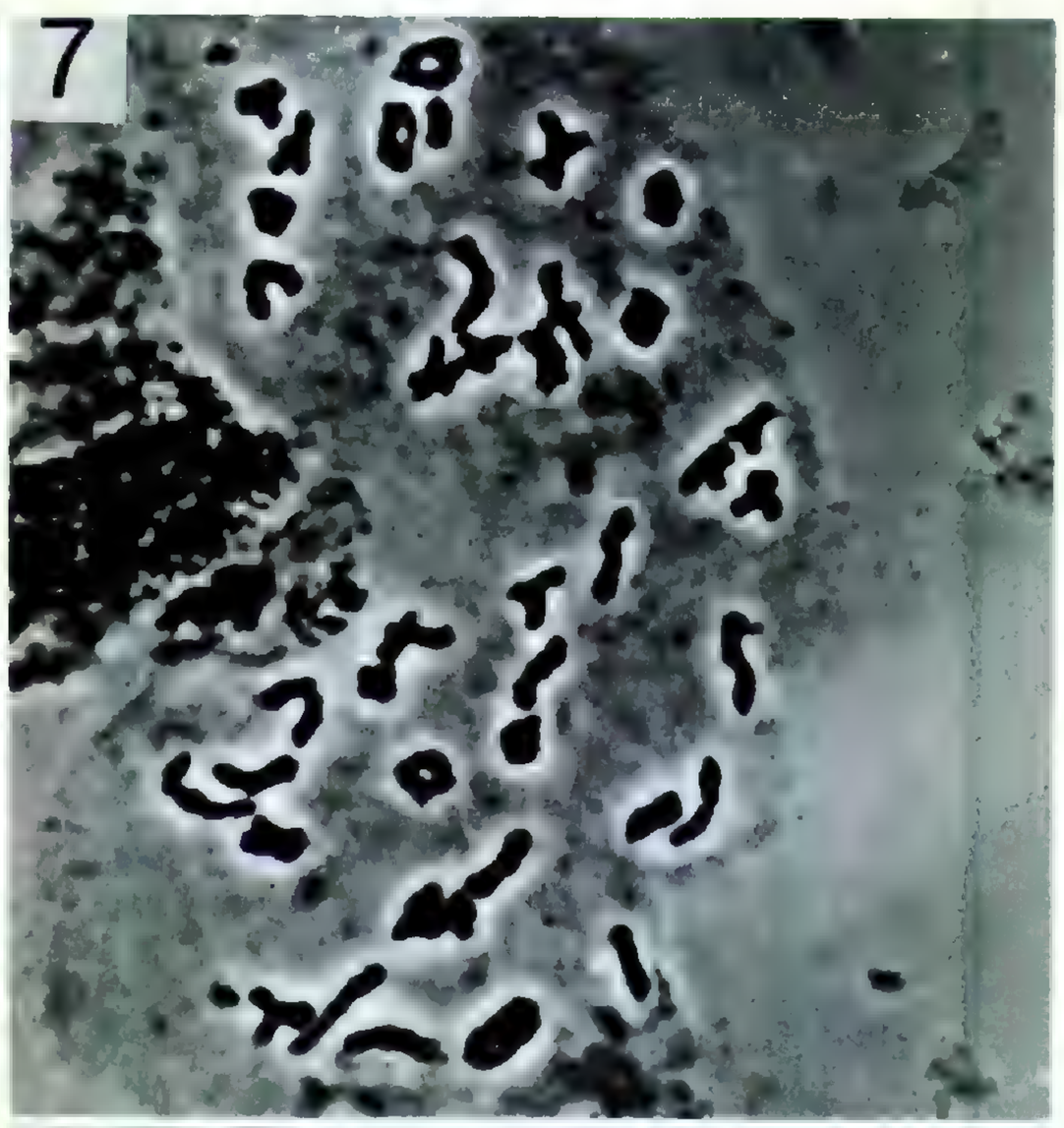

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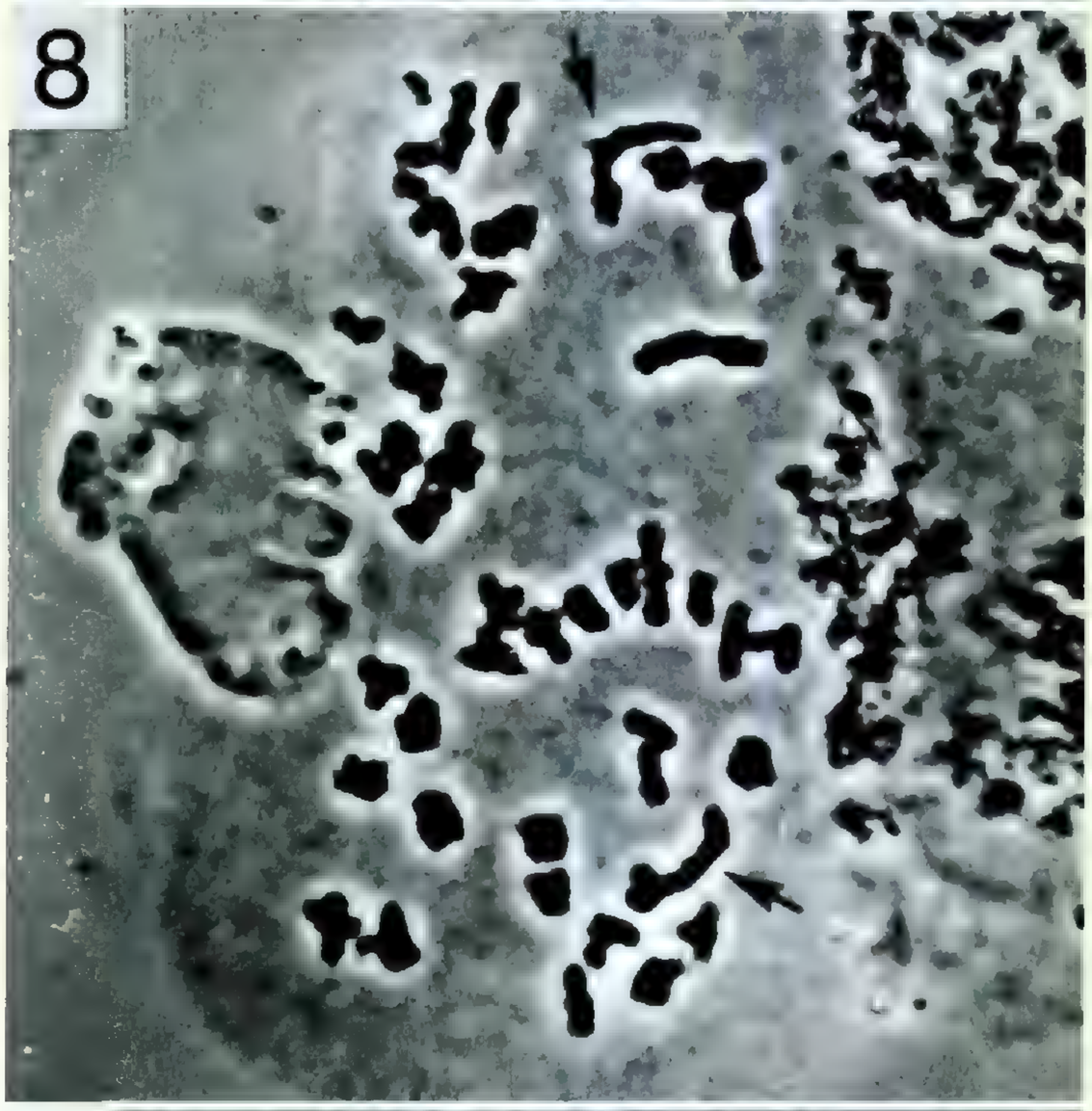

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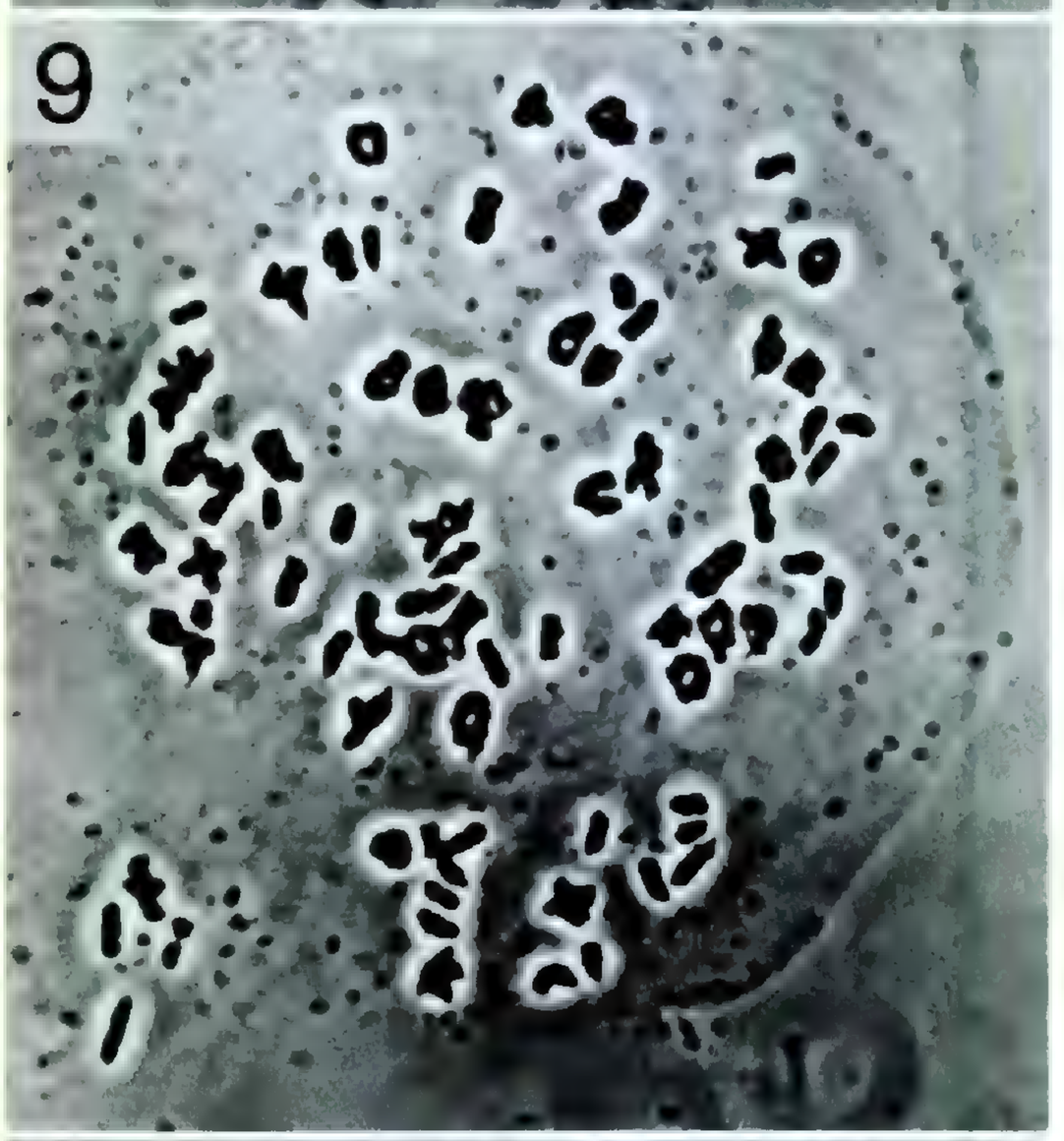

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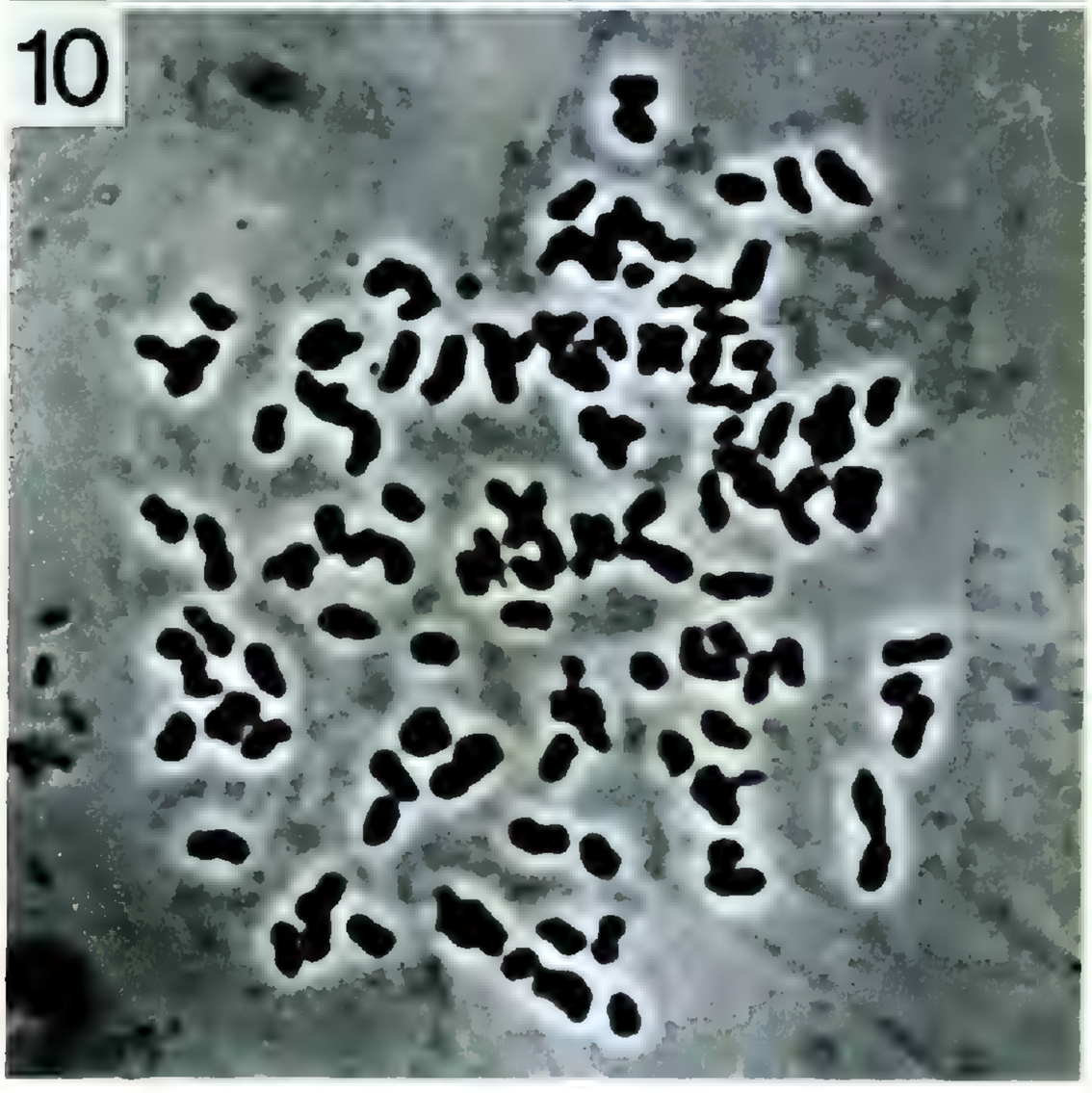

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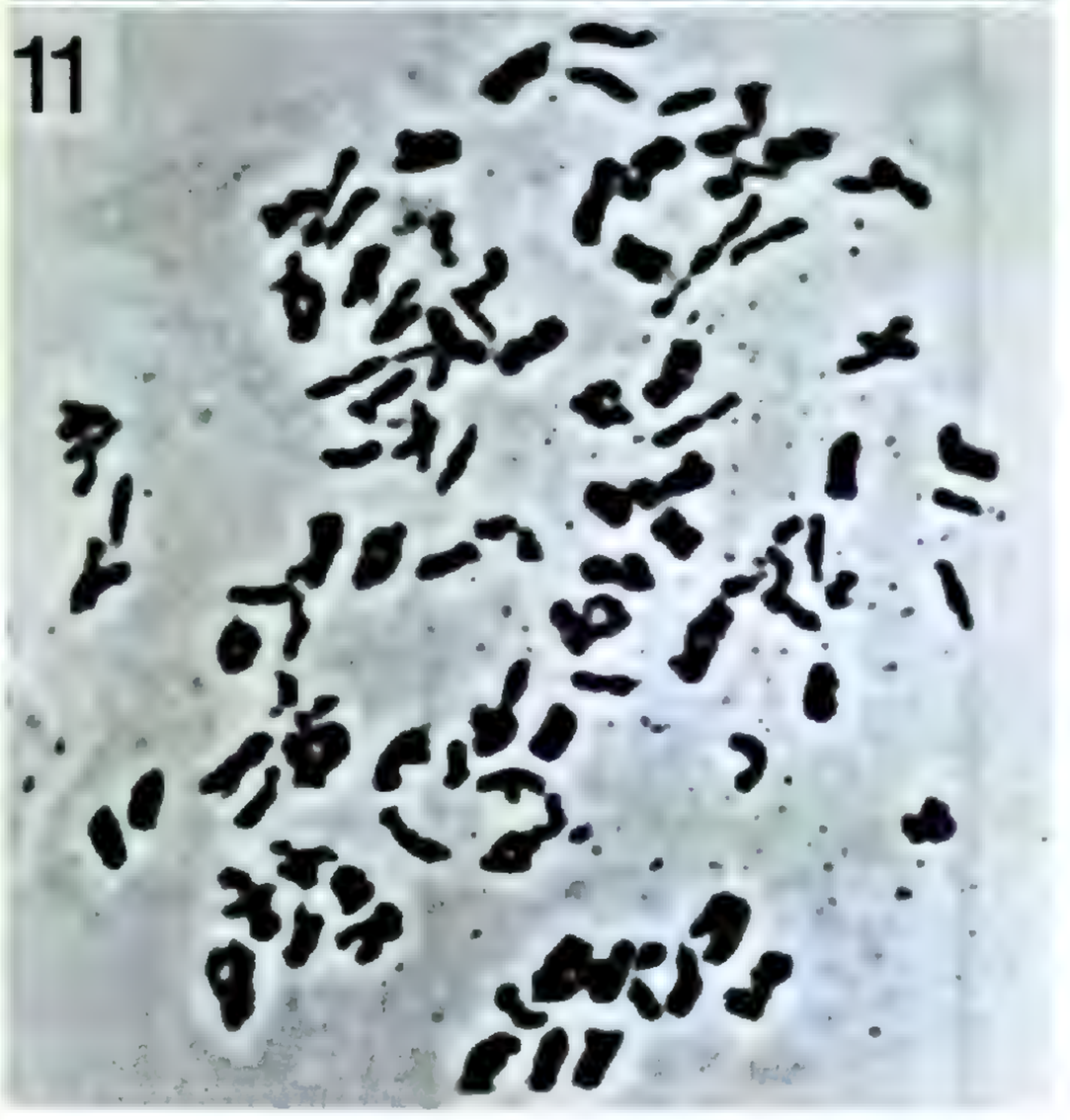

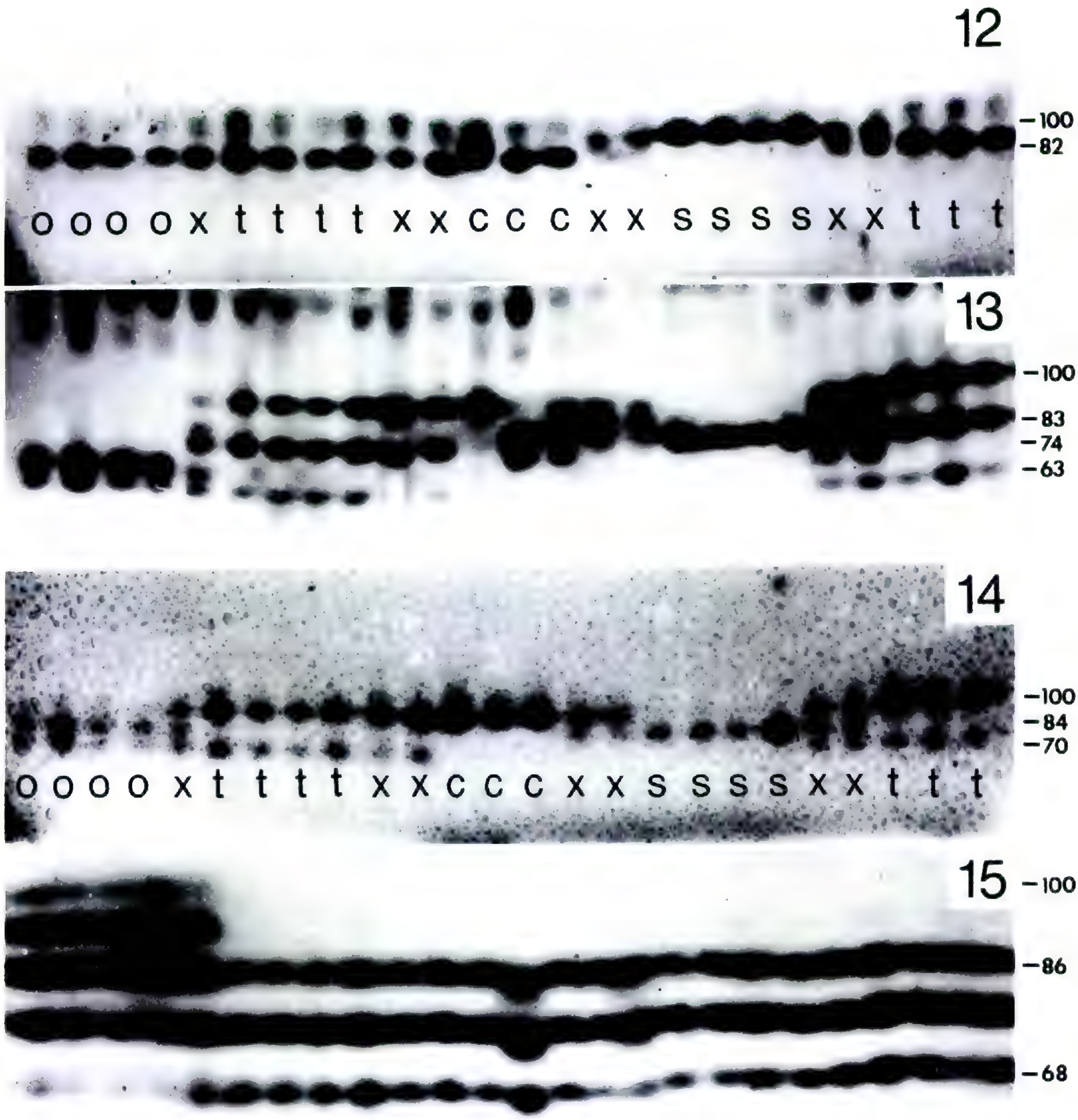

FIGURES 12–15. Isozymes of Costa Rican polystichums: c = *P. concinnum*, o = *P. orbiculatum*, s = *P. speciosissimum*, t = *P. talamancanum*, x = hybrid between adjacent species. Mobilities indicated to right of gels are average percents of fastest band at each locus. Barrington collection numbers for source plants for isozymes in order left to right (vouchers deposited at VT): o, *1273*, *1504*, *1509*, *978*; x, *1283*; t, *1263*, *1155*, *1270*, *1261*; x, *1244*, *1260*; c, *727*, *816*, *822*; x, *1274*, *1516*; s, *1513*, *1708*, *1704*, *1700*; x, *1500*, *973*; t, *1250*, *1280*, *1282*.—12. IDH.—13. PGI-2: *P. concinnum* shows three genotypes, two with the *P. concinnum* marker PGI-2^{100}; in *P. orbiculatum* × *P. talamancanum* note heterodimer combining PGI-2^{74} (*P. orbiculatum* marker) with PGI-2^{100} (*P. talamancanum* marker inherited from *P. concinnum*); in *P. speciosissimum* × *P. talamancanum* note heterodimers combining both PGI-2^{63} and PGI-2^{100} (*P. talamancanum* marker inherited from *P. concinnum*) with PGI-2^{83} (marker inherited from *P. speciosissimum*).—14. SkDH.—15. TPI-1: *P. orbiculatum* band interpretation—fixed heterozygote combines bands of unmodified allozymes 68 and 86 and their respective modified versions at 86 and 100 with all possible heterodimers. TPI-1^{86} co-migrates with the modified variant of TPI-1^{68}. Other taxa have only the slower triplet. Alternatively 86 and 100 are the unmodified products.

Each of the two tetraploid species consistently showed a single heterozygous banding pattern at loci with more than one allele. *Polystichum talamancanum* showed fixed heterozygous patterns at HK, LAP, MDH, PGI-1, PGI-2, and SkDH in all sampled plants. All sampled plants of *P. orbiculatum* showed fixed heterozygous expression at AAT, HK, LAP, PGI-1, PGI-2, PGM, SkDH, and TPI-1. Complexity of the fixed heterozygous pattern at TPI-1 is hypothesized to be increased by

post-translational modification, as discussed in Gastony (1988); see caption to Figure 15 for interpretation.

CHROMOSOME NUMBERS AND PAIRING BEHAVIOR OF HYBRIDS

The four putative hybrids from the Cerro de la Muerte were documented with information on chromosome number and pairing behavior. The hybrid between the two diploid species, *P. concinnum* and *P. speciosissimum*, was documented to be diploid based on counts of two hybrid individuals (*Barrington 705* and *1274*). Pairing was notably variable within individuals, ranging from 32 pairs and 18 univalents to 40 pairs and 2 univalents (Figs. 6, 7). Trivalents were also observed (Fig. 8). The hybrid between *P. concinnum* and *P. talamancanum*, based on chromosome counts of six individuals, is triploid with 41 pairs and 41 univalents at meiosis I (Fig. 9). The hybrid between *P. speciosissimum* and *P. talamancanum* is represented in this study by two individuals (*Barrington 973* and *1500*), the first of which yielded a triploid count of 31 pairs and 61 univalents in meiosis I (Fig. 10). The fourth hybrid, *P. orbiculatum* × *P. talamancanum*, is represented by a single individual, *Barrington 1283*. This hybrid yielded a tetraploid count of 51 pairs and 62 univalents in meiosis I (Fig. 11).

ISOZYME PATTERNS OF HYBRIDS

Hybrids have isozyme profiles consistent with their parentage as proposed from morphological criteria (Figs. 12–15). Based on two hybrid plants, *Barrington 1274* and *1516*, *Polystichum concinnum* × *P. speciosissimum* includes the marker bands of *P. concinnum* (PGI-2^{100} and SkDH^{100}) and *P. speciosissimum* (IDH-2^{100} and PGI-2^{83}). The hybrid between *P. concinnum* and *P. talamancanum* has the same diagnostic bands and fixed heterozygous loci as *P. talamancanum*, based on electrophoretic analysis of three individuals. Both individuals of *P. speciosissimum* × *P. talamancanum* include the marker bands reported for the proposed parents (IDH-2^{100} and PGI-2^{83} for *P. speciosissimum*; PGI-2^{100} and SkDH^{100} for *P. talamancanum*). *Polystichum orbiculatum* × *P. talamancanum* includes the diagnostic bands for *P. talamancanum* and *P. orbiculatum* (that is, PGI-2^{100} and SkDH^{100} shared with *P. talamancanum*, PGI-2^{63} and SkDH^{70} shared with both *P. talamancanum* and *P. orbiculatum*, and PGI-2^{74} and TPI-1^{86} shared only with *P. orbiculatum*).

DISCUSSION

INFERENCES ABOUT EVOLUTIONARY RELATIONSHIPS

Consideration of the cytological and electrophoretic data presented here leads to hypotheses for evolutionary relationships between *Polystichum* species on the Cerro de la Muerte (Fig. 1, Table 1). *Polystichum talamancanum* is an allotetraploid, since it has 82 pairs of chromosomes in meiosis I and its heterozygous banding patterns are all fixed. Corroborating evidence is available: the triploid *P. speciosissimum* × *P. talamancanum* consistently shows fewer than 41 pairs of chromosomes, suggesting that the hybrid combines three nonhomologous sets of chromosomes. Hence the two sets of chromosomes contributed by *P. talamancanum* are not homologous, so *P. talamancanum* must be an allotetraploid. Furthermore, because all marker allozymes for *P. concinnum* are included in the fixed heterozygous banding patterns of *P. talamancanum*, one of the progenitors of *P. talamancanum* is almost certainly *P. concinnum*. This interpretation is supported by the pairing pattern (equal number of univalents and pairs) in *P. concinnum* × *P. talamancanum*, typical of backcrosses between allotetraploids and their diploid progenitors. *Polystichum talamancanum* is almost certainly recent in origin, since its geographic range is highly restricted and coterminous with one of its progenitors (Stebbins, 1971).

Polystichum orbiculatum, a common alpine species from Bolivia to Mexico, is allotetraploid at Cerro de la Muerte; it shows the fixed heterozygous pattern typical of allopolyploids that combine different alleles from each of their diploid progenitors. *Polystichum orbiculatum*, as broadly circumscribed by recent taxonomists (Smith, 1981; Stolze, 1981), may also include one or both of its diploid progenitor species, since small-spored plants have been encountered in Venezuela (Barrington et al., 1986). A similar species perhaps involved in the ancestry of *P. orbiculatum* is *P. sodiroi* Christ of Ecuador, for which a diploid count of $2n = 82$ has been reported (Sorsa in Fabbri, 1965).

Polystichum orbiculatum evidently shares one parent with *P. talamancanum*, since a subset of marker allozymes is consistently shared by the two allotetraploid species. Corroborating evidence for this conclusion is the pairing pattern in *P. orbiculatum* × *P. talamancanum*. Its 51 pairs and 62 univalents are interpreted as representing two homologous sets of chromosomes, one contributed by each of the two tetraploids reported here, and two nonhomologous sets (some members of which

pair), representing a *concinnum* genome contributed by *P. talamancanum* and a genome of unknown origin contributed by *P. orbiculatum*. The two homologous sets, which undergo allosyndetic pairing in this hybrid, are presumably derived from a single diploid progenitor, so far not documented from the Cerro. This implication of a single diploid progenitor in the origin of more than one allotetraploid is a pattern already documented in the north temperate zone (e.g., *Dryopteris cristata* and *D. carthusiana*, Werth, 1989).

GENERAL SIGNIFICANCE

There is no evidence that the species on Cerro de la Muerte constitute a monophyletic group; on the contrary, there is ample morphological evidence that the diploid species present or implicated in the origin of hybrid species on the Cerro are members of different species groups with geographically disparate affinities. For instance, *Polystichum concinnum* is allied to the diverse complex of species from southern Mexico (Barrington, 1989), but *P. orbiculatum* is presumably Andean in origin (Barrington et al., 1986). Although *P. speciosissimum* is morphologically distinct enough to have been recognized as a monotypic species of the genus *Plecosorus*, its chromosome behavior in meiosis I suggests that it is not strongly differentiated from the remainder of the taxa here. Even in a large and morphologically diverse genus like *Polystichum*, hybridization and polyploidy depend on geographic and ecological proximity. The scope of *Polystichum* species involved in secondary interactions is not limited by phylogenetic proximity (as inferred from morphology).

A high frequency of homoeologous pairing is documented here for hybrids between tropical-montane *Polystichum* species, just as it was for north temperate hybrids (Wagner, 1973). There is also notable variation in pairing in these hybrids. Furthermore, degree of homoeologous pairing in hybrids is independent of morphological similarity in these species. Especially telling is the hybrid between *Polystichum concinnum* and *P. speciosissimum*, which shows virtually complete pair formation in some cells although the progenitor species are strongly differentiated morphologically (Barrington, 1985b). This emerging picture of unusual residual homology (homoeology), typical in *Polystichum* but rare elsewhere in the Polypodiales, may reflect one of two cytological phenomena. It is possible that divergence of whole genomes is not so great in *Polystichum* species as in other genera of ferns, in which case the genus has a noteworthy place in studies of fern evolution. Alternatively, pairing may be under less stringent genetic control in *Polystichum* than in other fern groups, thus permitting the relatively high frequency of homoeologous pairing observed in *Polystichum* hybrids (Wagner, 1973; Barrington, 1986).

The pattern of interactions among *Polystichum* species in high-montane Costa Rica emerging from this work and from earlier papers is notable for its similarity to patterns of hybridization and speciation in north temperate ferns in the Dryopteridaceae, Aspleniaceae, and other groups (Lovis, 1977; Barrington et al., 1989). The ecology of interaction among species (Barrington, 1985b), the morphology of the hybrids and hybrid species (Barrington, 1985a, b, 1989), the basic features of chromosome behavior at meiosis I, and isozyme patterns are all similar to those seen in north temperate polyploid complexes. Since Pleistocene climatological change was significant in tropical America (van der Hammen, 1974), vegetational change and ecological disturbance in the Sierra Talamanca may have been qualitatively like that in the north temperate zone. Hence, similar Pleistocene climatological history may be the underlying determinant of speciation phenomena in the genus *Polystichum* in both regions.

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ELECTROPHORETIC EVIDENCE FOR ALLOTETRAPLOIDY WITH SEGREGATING HETEROZYGOSITY IN SOUTH AFRICAN *PELLAEA RUFA* A. F. TRYON (ADIANTACEAE)[1]

Gerald J. Gastony[2]

Abstract

Pellaea rufa is a sexually reproducing tetraploid species with a chromosome number of $n = 58$ II at meiosis. Unlike previously reported tetraploid ferns, sporophytes of *P. rufa* exhibit substantial intrapopulational electrophoretic variation for respective enzyme phenotypes, and many of their heterozygous phenotypes are segregating rather than fixed. Two hundred and twenty individual gametophytes from a tetraploid sporophyte heterozygous for four alleles at the PGI-2 locus were subjected to electrophoresis to determine whether inheritance is tetrasomic as expected in an autotetraploid or disomic as expected in an allotetraploid. Results reject the hypothesis of autotetraploidy but fit expectations under the hypothesis that *P. rufa* is an allotetraploid with fixed intergenomic heterozygosity and segregating intragenomic heterozygosity. Observed intragenomic heterozygosity is consistent with a direct hybrid origin of allotetraploid *P. rufa* via gametes from unreduced spores and with a more probable indirect origin involving unreduced spores from intermediate allodiploids. Disomic inheritance of intragenomic heterozygosity generates electrophoretic variation in *P. rufa* that is less than that in autopolyploids with polysomic inheritance but greater than that previously reported in allopolyploids.

Pellaea rufa A. F. Tryon is endemic to xeric areas of the southern Cape Province of South Africa (Anthony, 1984; Schelpe & Anthony, 1986) and is the only species of *Pellaea* sect. *Pellaea* with a non-American distribution (Tryon, 1957). Until Tryon (1955) recognized their morphologically distinctive features, these African plants were considered conspecific with *P. andromedifolia* (Kaulf.) Fée from California and Baja California Norte.

Tryon (1955, 1957) had no living material of *P. rufa* from which chromosome counts could be made. She noted, however, that sporophytes have 64-spored sporangia, the number typical of sexually reproducing diploid species of *Pellaea*, as opposed to the 32-spored condition characteristic of agamosporous taxa that are typically triploid or tetraploid in this genus (Tryon & Britton, 1958; Tryon, 1968). Three recent floristic works (Jacobsen, 1983; Anthony, 1984; Schelpe & Anthony, 1986) included treatments of *P. rufa*, but offered no observations regarding its chromosome number or reproductive biology. Tryon's (1955, 1957) and Anthony's (1984) observations of 64 spores per sporangium therefore stand alone in suggesting that this species is a normal, sexually reproducing diploid like most populations of *P. andromedifolia*, its putative close relative in California. This paper presents both cytological and isozymic evidence that *P. rufa* is tetraploid and analyzes its segregating electrophoretic phenotypes to determine whether it had an autopolyploid (intraspecific) or allopolyploid (interspecific) origin.

Materials and Methods

Live sporophytes of *Pellaea rufa* A. F. Tryon grown in the Indiana University greenhouses were

[1] This paper is dedicated to Dr. Rolla M. Tryon, Jr., and Dr. Alice F. Tryon to whom I am grateful for the graduate training that makes my research possible. I thank Nicola C. Anthony and P. Anne Bean for supplying live specimens of *Pellaea rufa*, Valerie R. Savage for meticulous help as laboratory technician, Marcus C. Rhoades, Ellen Dempsey, and Drew Schwartz for discussions of cytogenetics, and the National Science Foundation for support under grant BSR 8516666. I acknowledge helpful reviews of this paper by C. H. Haufler and C. R. Werth.

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obtained from four native populations in the Cape Province of South Africa ("sporophytes" below). Additional accessions of sporophytes from these populations did not survive transport to Indiana and were instead analyzed via families of gametophytes grown from their spores ("gametophyte families" below). These four populational sources are (1) Klipbank (grid reference 3222AD), five sporophytes; (2) Skeiding (grid reference 3320BA), 14 sporophytes and 10 gametophyte families; (3) Die Hel (grid reference 3321BC), seven sporophytes and 18 gametophyte families; (4) Boonstevlei (grid reference 3220DD), 22 sporophytes and 13 gametophyte families. Specimens of *P. andromedifolia* used in Figures 5 and 6 are from populations 2, 5, 6, 7, and 11 of Gastony & Gottlieb (1985). Voucher specimens are deposited at IND. For meiotic chromosome squashes, portions of sporophylls were fixed at 21°C in 3 : 1 absolute alcohol : glacial acetic acid for at least 24 hours. Sporangia were then removed individually and squashed following Manton's (1950) acetocarmine technique. For mitotic chromosomes, root tip squashes were prepared as in Roy & Manton (1965) using glusulase obtained from DuPont pharmaceuticals. Electrophoresis and staining methods were as in Soltis et al. (1983), using 12.8% starch and the tris-HCl grinding buffer with 12% PVP. Single gametophytes were subjected to electrophoresis as in Gastony & Gottlieb (1982) except that each was ground with one or two drops of grinding buffer from the tip of a Pipetman 100 in its own well in a porcelain spot plate (mortar) using a small glass test tube as a pestle. Shikimate dehydrogenase (SkDH) was resolved on gel and electrode system 2, and phosphoglucoisomerase (PGI) was resolved on system 7. Allozymes are labeled with the most anodally migrating one designated A, the next most anodal labeled B, etc., and with the corresponding coding alleles labeled *a*, *b*, etc.

Results and Discussion

CHROMOSOME COUNTS

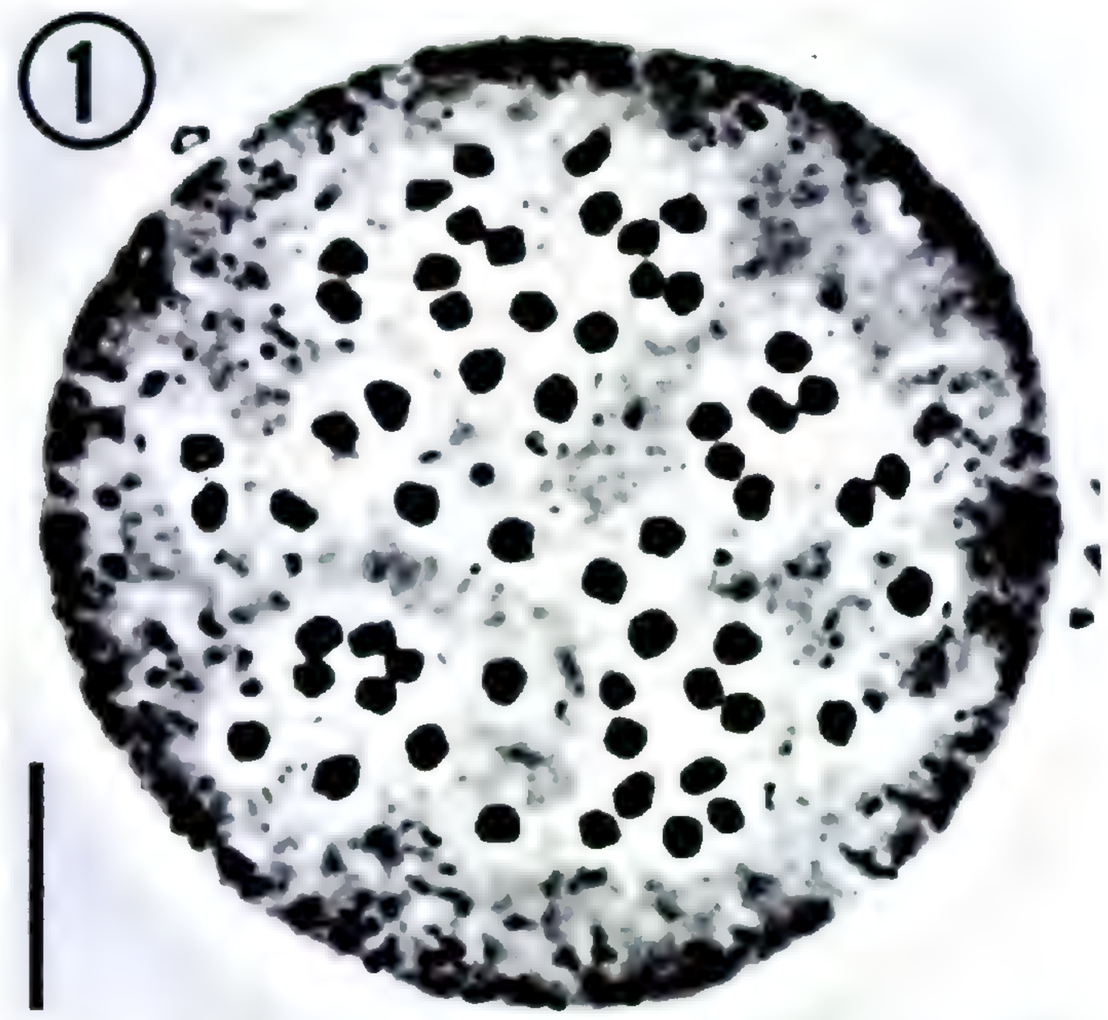
Recently obtained living sporophytes of *P. rufa* have provided the first chromosome counts for this species, showing that it is tetraploid, not diploid, with $n = 58$ II at meiosis (Figs. 1–3). Counts of approximately 116 mitotic chromosomes (Fig. 4) in several cells from root tips confirm this tetraploidy and demonstrate the normal alternation of 116 mitotic chromosomes and 58 meiotic bivalents expected with 64-spored sexually reproducing tetraploids.

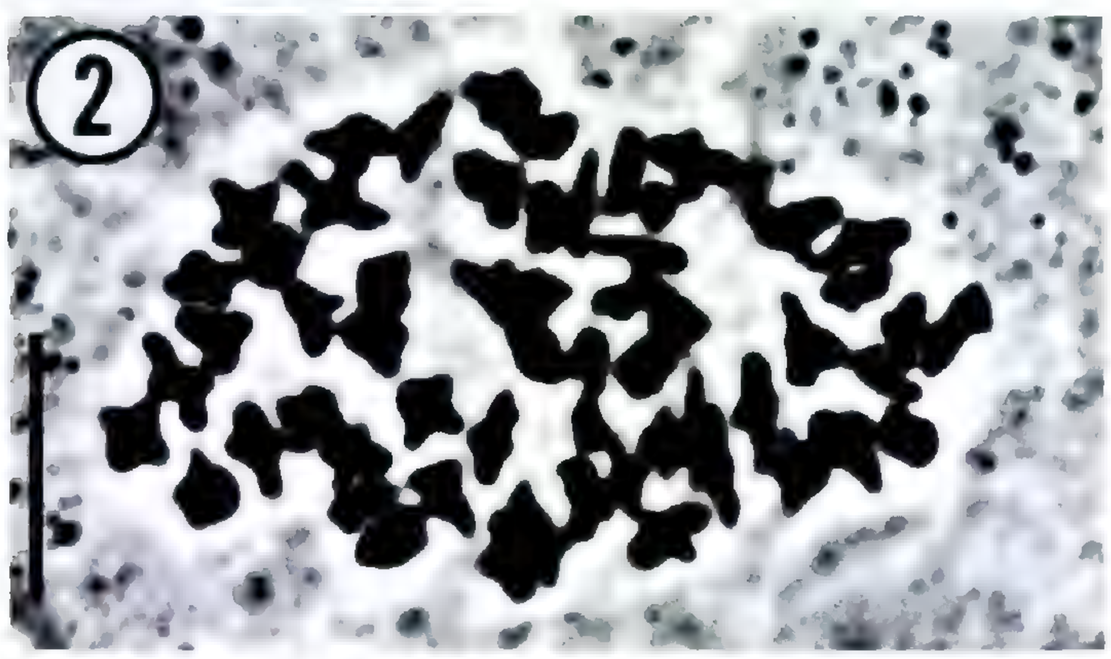
ELECTROPHORESIS

Studies of electrophoretic isozyme patterns were initiated as part of an ongoing study of the light-stiped species of *Pellaea* sect. *Pellaea*. In *P. rufa*, these revealed the complex enzyme phenotypes expected from tetraploids with up to four alleles per enzyme locus. Results for the monomeric enzyme SkDH and the dimeric enzyme PGI illustrate these findings.

For SkDH, diploid sporophytes of *P. andromedifolia* (Fig. 5, lanes AND) exhibit a single allozyme band when they are homozygous and two bands of equal staining intensities when they are heterozygous at this locus (Gastony & Gottlieb, 1982). All other lanes in Figure 5 are a random selection of sporophytes of tetraploid *P. rufa* from four different populations. Only four of these 23 sporophytes of *P. rufa* (17%) are one-banded as expected of plants homozygous at this locus, whereas 83% of them are at least two-banded and therefore heterozygous at this locus. Allozymes A, B, C, and D are coded at this locus (Fig. 5), and two of these sporophytes encode three allozymes at the *Skdh* locus, manifesting the extra heterozygosity per locus expected in tetraploids.

PGI is expressed as chloroplastic and cytosolic isozymes (Gastony & Darrow, 1983). PGI-1, the chloroplastic more anodal isozyme (Fig. 6), is not well resolved in species of *Pellaea* and is not discussed further. A diversity of patterns is expressed for the cytosolic cathodal isozyme (PGI-2) in *P. rufa*. Lanes 7–11 (AND) of Figure 6 are from diploid sporophytes of Californian *P. andromedifolia*, which expresses the normal diploid complement of two copies of the locus coding PGI-2, one in each of its chromosome sets. Diploids homozygous at the locus coding this dimeric enzyme (lanes 7, 8, 10, 11) express a single homodimeric allozyme band, whereas diploids heterozygous at this locus (lane 9) exhibit a three-banded pattern of symmetrical staining intensities with outer homodimeric bands and a central heterodimeric band combining the monomeric subunits coded by both alleles (Gastony & Gottlieb, 1982). Tetraploid sporophytes of *P. rufa* have four copies of the *Pgi-2* locus, one copy in each chromosome set. These tetraploids express up to four homodimeric PGI-2 allozymes (Figs. 6 and 7, bands AA, BB, CC, DD) plus heterodimeric bands in all possible combinations (six bands: AB, AC, AD, BC, BD, CD), so that a sporophyte heterozygous for all four alleles expresses ten bands very closely spaced, as in Figure 6 lane 4 and Figure 7 lane 2 (in both figures, heterodimeric bands AD and BC are contiguous



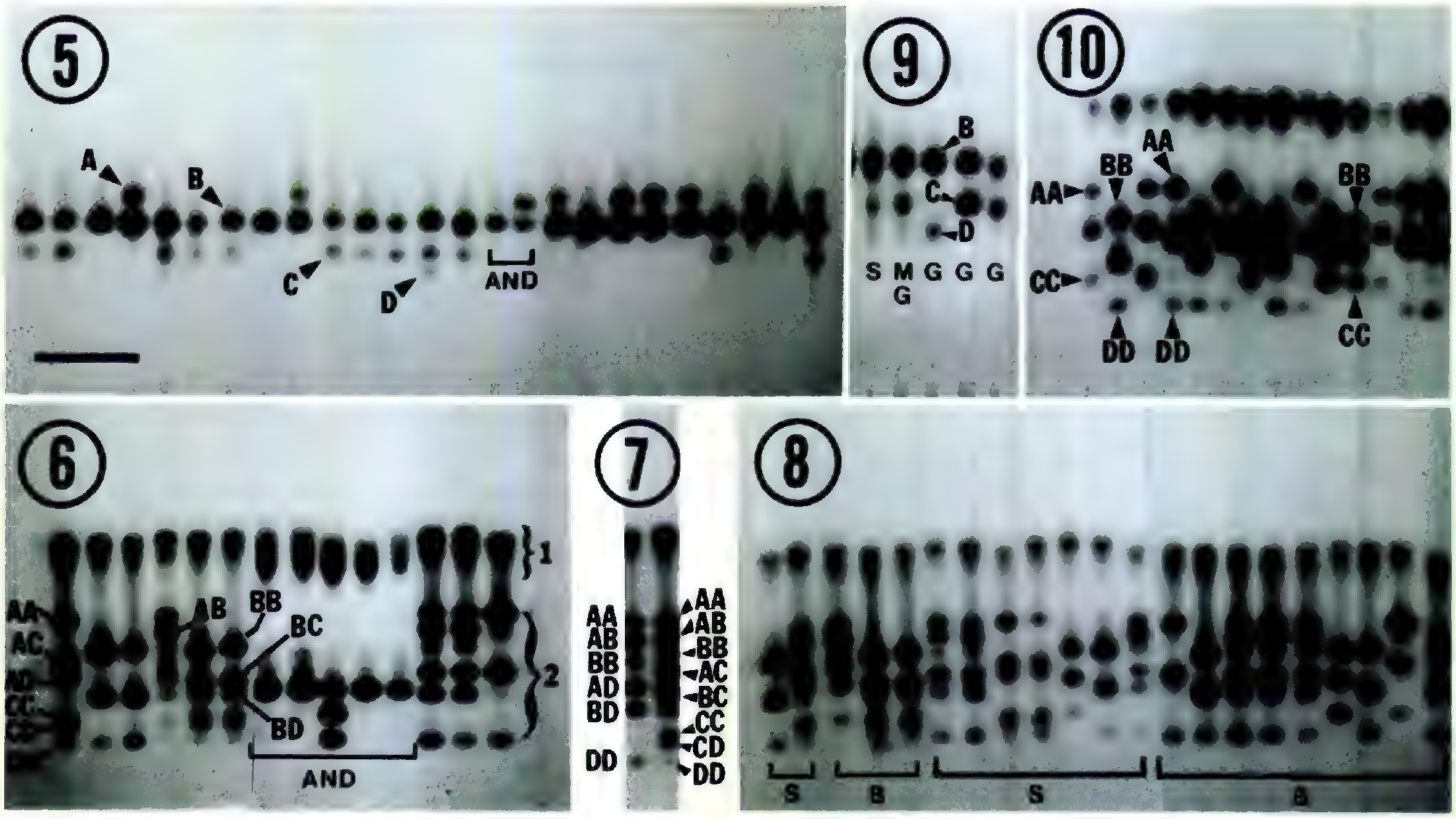


FIGURES 1–4. Chromosomes of *Pellaea rufa*. —1, 2. Meiotic chromosomes showing $n = 58$ II, from Boonstevlei sporophytes B-39 and B-1 respectively. —3. Camera lucida drawing interpreting areas of overlap in Figure 2. —4. Mitotic chromosomes showing $2n =$ ca. 116 in Skeiding sporophyte S-8. Scale bars = 0.01 mm.

and partially overlapping, and heterodimeric band CD is contiguous with faint homodimeric band CC). Allozymes specified by alleles *b*, *c*, and *d* are often more weakly expressed than those specified by allele *a* even when these alleles are present in equal doses, as in the sporophyte in Figure 6 lane 4 and Figure 7 lane 2 whose *Pgi-2* genotype is *abcd* as shown below.

The occurrence of tetraploid sporophytes with varying electrophoretic phenotypes for SkDH and PGI in *P. rufa* was unexpected. In previous studies of polyploid ferns, all sporophytes in a given population have been monomorphic for each enzyme pattern, except for occasional individuals with variant phenotypes attributed to independent allopolyploid origins from parental diploids of variant genotype, or to mutations, or to rare recombinational events involving pairing among homoeologues in the polyploids (e.g., Werth et al., 1985b). Such phenotypic monomorphism was explained in the classic study of *Tragopogon* by Roose & Gottlieb (1976), where allotetraploids exhibit additive expression of the bands coded by the divergent genomes of their diploid progenitors. The allodiploid hybrid inherits the variant alleles at the enzyme loci of both progenitor species and expresses both allozymes. By doubling its chromosomes, the allodiploid becomes an allotetraploid in which the chromosomes of each parental genome have identical mates with which they preferentiallly pair at meiosis. Intragenomic pairing of the doubled chromosomes precludes genetic segregation, all meiotic products maintain the intergenomic heterozygosity of the allotetraploid sporophyte, and the fixed heterozygous enzyme phenotypes in the population are thereby perpetuated generation after generation.

Similar fixation (nonsegregation) of enzyme phenotypes in previously studied polyploid ferns is reported in the study of the Appalachian *Asplenium* complex by Werth et al. (1985a, b) and in Haufler's (1985) study of tetraploid *Cystopteris fragilis*. In both of these studies, as in that of Roose & Gottlieb (1976), lack of segregation of heterozygous enzyme phenotypes in allotetraploid taxa is attributable to the fact that heterozygosity is intergenomic whereas chromosome pairing is intragenomic, between the doubled chromosomes within each of the two divergent genomes inherited from the diploid progenitor species.



FIGURES 5–10. Electrophoretic SkDH and PGI banding patterns of *Pellaea rufa* and *P. andromedifolia*. In all figures, the anode is toward the top and origin is at the bottom. Scale bar = 1 cm and serves Figures 5–10.—5. Monomeric allozymes A, B, C, D constituting variant SkDH phenotypes of randomly selected tetraploid sporophytes from four populations of *P. rufa*, except for diploid sporophytes of *P. andromedifolia* in lanes AND.—6. Homodimeric and heterodimeric allozymes constituting variant phenotypes of PGI-2 (PGI-1 inadequately resolved) in randomly selected tetraploid sporophytes from four populations of *P. rufa*, except for diploid sporophytes of *P. andromedifolia* in lanes AND.—7. Clarification of the four homodimeric and six heterodimeric bands of PGI-2. Because of congestion, heterodimeric bands AD and BD are not labeled in the right lane but are identifiable by comparison with their counterparts in the left lane. Bands AD and BC are contiguous and partially overlapping, and bands CC and CD are contiguous.—8. Variant PGI phenotypes of randomly selected sporophytes from the Skeiding (S) and Boonstevlei (B) populations of *P. rufa*.—9. Three-banded SkDH phenotype in a sporophyte (S) of *P. rufa* and in an extract of mixed gametophytes (MG) from that sporophyte, with segregation of two-banded patterns in single gametophytes (G).—10. Segregation of homodimeric PGI-2 phenotypes AA/CC, AA/DD, BB/CC, BB/DD (with respective heterodimeric bands AC, AD, BC, BD unlabeled) in gametophytes from a sporophyte with the phenotype of Figure 6 lane 4 and Figure 7 lane 2.

Heterozygous electrophoretic phenotypes are also fixed in polyploid agamosporous fern taxa with the Döpp-Manton type of sporogenesis (Gastony & Gottlieb, 1985; Gastony, 1988; Gastony & Windham, 1989). Sporophytes of these taxa produce viable spores via modified sporogenesis (Manton, 1950) in which the final mitotic division before meiosis is endomitotic. This yields restitution nuclei of doubled ploidy in which each chromosome has a mitotically derived, duplicate sister chromosome with which to pair. Because pairing is restricted to these genetically identical sister chromosomes (Lovis, 1977), there is no genetic segregation at meiosis. As reported in allopolyploid *Asplenium* species and allotetraploid *Cystopteris fragilis*, the banding patterns of agamosporous sporophytes are invariantly expressed in their individual gametophytes and in the sporophytes they in turn beget.

Contrary to the findings of these previous studies, diverse enzyme phenotypes are seen among sporophytes from single populations of tetraploid *P. rufa* (Fig. 8), and many of the heterozygous electrophoretic phenotypes do segregate, indicating an intralocus component to the heterozygosity. For example, three-banded (BCD) SkDH patterns of *P. rufa* sporophytes (Fig. 9, S), maintained when several randomly selected gametophytes are combined for electrophoresis (Fig. 9, MG), segregate phenotypes BD and BC in single gametophytes (Fig. 9, G).

Similarly, single gametophytes from sporophytes with the PGI-2 phenotype seen in Figure 6 lane 4 and Figure 7 lane 2 segregate diverse banding patterns for PGI-2 (Fig. 10). Thus, unlike previous reports for polyploid ferns, heterozygous banding patterns in tetraploid *P. rufa* are coded by up to four alleles per enzyme locus, and these alleles and their coded allozymes do segregate. Meiotic segregation of these genotypes into spores and derivative gametophytes and the subsequent random

recombination of gametophytic genotypes into sporophytes at fertilization accounts for the diversity of PGI-2 phenotypes seen among sporophytes within single populations.

Tetrasomic inheritance of segregating allozyme markers is increasingly invoked as evidence that tetraploid populations of various angiosperm species are autotetraploid (Soltis & Rieseberg, 1986; Soltis & Soltis, 1988, 1989; Rieseberg & Doyle, 1989; Wolf et al., 1989). Tetrasomic inheritance is to date unreported in pteridophytes (Werth, 1989). Because *P. rufa* provides the first reported instance of regularly occurring segregation of electrophoretic phenotypes in natural populations of tetraploid ferns, it is of interest to determine whether this species exhibits tetrasomic inheritance, a corollary of autopolyploidy (intraspecific polyploidy) as discussed in Soltis & Rieseberg (1986), Soltis & Soltis (1989), and Wolf et al. (1989), or disomic inheritance as expected from allopolyploidy (interspecific polyploidy).

In ferns, autotetraploidy may result when a normal diploid sporophyte produces unreduced spores whose diploid gametophytes self-fertilize or cross-fertilize with another diploid gametophyte from the same sporophyte or from a different sporophyte of the same species. Alternatively, an unreduced diploid gametophyte may cross with a normal haploid gametophyte of the same species to yield an autotriploid sporophyte. If the autotriploid produces unreduced spores, the triploid gametophytes may cross with a normal haploid gametophyte of the same species to yield an autotetraploid by this less direct route (see discussion of these processes in Haufler et al., 1985; Gastony, 1986). In such cases, the progenitor diploid sporophytes have two homologues for each kind of chromosome, and those homologues pair regularly as bivalents at meiosis. Gametophytes from the unreduced diploid spores of those sporophytes carry the same pairable sets of homologous chromosomes, and when these unreduced gametophytes cross as noted above, the resulting triploid or tetraploid sporophyte has three or four homologues respectively for each chromosome. Because each of these homologues is capable of pairing with the others, some degree of multivalent chromosome pairing is generally expected in autotetraploids (Stebbins, 1947; Jackson & Casey, 1982). Although only bivalent pairing has been observed in *P. rufa*, lack of multivalents cannot be regarded as evidence against autopolyploidy in this species, because bivalent formation appears to be under genetic control in autopolyploid ferns (see review in Lovis, 1977; Gastony & Windham, 1989). Genetic control is shown, for example, in an agamosporous triploid species in which some sporangia have one endomitotic division and others have two successive endomitotic divisions preceding meiosis (Windham, pers. comm.). Chromosome pairing is strictly bivalent in the latter sporangia, although the same genome is represented at least four and possibly twelve times in them. Although only bivalents form in autotetraploid ferns, pairing partners are expected to be randomly chosen from among the homologues, with resultant tetrasomic inheritance. Such random pairing is expected because the multiple homologues resulting from unreduced spores should be indistinguishable except inasmuch as they may carry different alleles at a given locus—a factor that does not affect pairing potential in Mendelian genetics.

If *P. rufa* is autotetraploid, sporophytes should exhibit tetrasomic inheritance when single gametophytes derived from their spores are analyzed electrophoretically. If it is allotetraploid, sporophytes should exhibit disomic inheritance with segregation restricted to whatever intralocus heterozygosity may be present within each ancestral genome. Because autopolyploidy and allopolyploidy predict different genotypic results in gametophytic progeny, critical analysis of genetic segregation can be used to test the nature of polyploidy in *P. rufa*. Tetrasomic inheritance in an autotetraploid with random bivalent pairing and no crossing over between the *Pgi-2* locus and the centromere would yield six classes of gametophytic genotypes from a tetraploid sporophyte like that in Figure 6 lane 4 and Figure 7 lane 2 with genotype *abcd*: *ab*, *ac*, *ad*, *bc*, *bd*, *cd*. If the *Pgi-2* locus is sufficiently distant from the centromere that crossing over can occur betwen them, chromatid recombination could generate four additional gametophytic genotypes (*aa*, *bb*, *cc*, *dd*) so that tetrasomic inheritance should then yield ten classes of gametophyte genotypes: *ab*, *ac*, *ad*, *bc*, *bd*, *cd*, *aa*, *bb*, *cc*, *dd*. Because the position of the *Pgi-2* locus relative to the centromere is unknown in *P. rufa*, six to ten classes of gametophytes should be expected if a sporophyte of *P. rufa* with *Pgi-2* genotype *abcd* is autotetraploid. In the absence of recombination, the six classes noted above should occur with equal frequencies.

With disomic inheritance in an allotetraploid, the genotypes of the gametophytes derived from an *abcd* sporophyte will depend on how the four alleles are distributed within the sporophyte's two ancestral genomes. Three different distributions are possible, each with its respective set of gametophytic genotypes: (1) *ab* in one progenitor genome and *cd* in the other would yield gametophytic classes

ac, *ad*, *bc*, *bd*; (2) *ac* in one genome and *bd* in the other would yield gametophytic classes *ab*, *ad*, *cb*, *cd*; (3) *ad* in one genome and *bc* in the other would yield gametophytic classes *ab*, *ac*, *db*, *dc*. No matter how these alleles are distributed in the ancestral sporophytic genomes, chromosome pairing will be intragenomic, and this will yield only four classes of gametophytes. Chromatid recombination will not create more than four classes of gametophytes in the case of an allotetraploid with bivalent pairing. An allotetraploid not entirely restricted to preferential intragenomic pairing might engage in some random bivalent pairing or quadrivalent pairing (if bivalent pairing were not under genetic control), with segregational results approaching those of an autotetraploid. In that case, an allotetraploid could generate six or more classes of gametophytes and would be indistinguishable from an autotetraploid. Because only bivalents have been observed at meiosis in the sporophytes examined (e.g., Figs. 1–3), quadrivalent pairing in *P. rufa* is not likely. It is possible, however, that brief quadrivalent pairing at an early stage of prophase has gone unnoticed. Therefore if six or more classes of gametophytes are observed, further effort would be required to distinguish between the hypotheses of autopolyploidy and allopolyploidy. On the other hand, if no more than four classes of gametophytes are found in a large sample, inheritance is disomic and *P. rufa* is allotetraploid with intragenomic bivalent pairing.

Two hundred and twenty single gametophytes derived from a sporophyte with PGI-2 genotype *abcd* and the phenotype seen in Figure 6 lane 4 and Figure 7 lane 2 were subjected to electrophoresis and assayed for PGI-2. Only four classes of gametophytic phenotypes were observed: AA/CC, AA/DD, BB/CC, and BB/DD (each with its respective heterodimeric band; Fig. 10). The classes that were not observed are noteworthy. No gametophytic phenotypes corresponding to genotypes *aa*, *bb*, *cc*, or *dd* were observed. Those four phenotypes should have been observed if *P. rufa* were an autotetraploid with random bivalent pairing and with crossing over between the PGI-2 locus and the centromere. Furthermore, no gametophytic phenotypes corresponding to genotypes *ab* and *cd* were observed. Those two classes should have been observed if *P. rufa* were autotetraploid with random bivalent pairing and with no crossing over between the PGI-2 locus and the centromere. The absence of these six progeny classes rejects the hypothesis that *P. rufa* is autotetraploid.

Moreover, because paired homologues separate at the first division of meiosis, unobserved classes AA/BB and CC/DD are precisely those that should be lacking if alleles *ab* are in one ancestral genome and alleles *cd* are in the other ancestral genome of an allotetraploid with bivalent pairing restricted to intragenomic homologues. The observed absence of gametophytic classes AA/BB and CC/DD is therefore predicted by the hypothesis that *P. rufa* is allotetraploid with disomic inheritance resulting from exclusively intragenomic bivalent pairing. Finally, if the allotetraploid hypothesis is correct, the four observed classes of gametophytes are the only ones expected, and they should occur in equal frequencies in a large enough sample. The frequencies of the four observed classes of gametophytes were AA/CC = 49, AA/DD = 55, BB/CC = 55, and BB/DD = 61. A Chi-square test indicates that these results are not statistically different from the ratio of 1 : 1 : 1 : 1 expected for these 220 gametophytes ($\chi^2 = 1.309$, $P > 0.70$). *Pellaea rufa* is therefore accepted as an allotetraploid species. Furthermore, it is the first electrophoretically demonstrated example of an allopolyploid fern species in which fixed intergenomic heterozygosity is associated with segregating intragenomic heterozygosity. Several species of *Pellaea* that might have been involved in an allopolyploid origin of *P. rufa* occur in South Africa (Anthony, 1984), but they are currently placed in sect. *Holochlaena* (Tryon & Tryon, 1982).

Although the segregational data from *P. rufa* appear to fit all expectations for an allotetraploid, it has been suggested (Haufler, pers. comm.) that the *abcd Pgi-2* genotype of *P. rufa* may nevertheless have had an autopolyploid (intraspecific) origin. If a single diploid species ancestral to *P. rufa* contained alleles *a*, *b*, *c*, and *d* at *Pgi-2*, a given diploid sporophyte may have been heterozygous for alleles *ab* and another may have been heterozygous for alleles *cd*. Endomitotic divisions prior to sporogenesis in these sporophytes would yield unreduced diploid spores, gametophytes, and gametes such that an egg carrying *Pgi-2* alleles *ab* could be fertilized by a sperm carrying alleles *cd*, yielding an autotetraploid sporophyte with *Pgi-2* genotype *abcd*. The four observed classes of gametophyte progeny discussed above (Fig. 10: AA/CC, AA/DD, BB/CC, BB/DD) could be imagined to result from such an autotetraploid sporophyte if meiotic chromosome pairing were genetically restricted to bivalents in which pairing partners are not random, as expected in autotetraploids (Wolf et al., 1989), but invariably limited to chromosome pairs *a*/*b* and *c*/*d*. Such restricted pairing would be identical to what is expected and observed in allotetraploids, where preferential intragenomic

pairing is attributable to differences between the diverged genomes of the two progenitor species. This hypothesis that *P. rufa* may be an autotetraploid with preferential bivalent pairing seems implausible for two reasons. (1) In an autotetraploid, the four homologous chromosomes would be derived from the pairable parental diploid chromosomes that differ only in their alleles at the *Pgi-2* locus. Thus there is no reason to assume that pairing would be restricted to only one of the three combinations possible with four homologous chromosomes. On the other hand, the observed segregations are readily explained by allotetraploid pairing behavior well known in ferns. (2) This hypothesized autotetraploid origin of the original *abcd* sporophyte involves the improbable simultaneous occurrence of three rare events: two independent cases of unreduced spore formation in sporophytes with complementary variant genotypes and intergametophytic crossing between the resulting unreduced gametophytes.

If the interspecific diploid sporophytic progenitors of allotetraploid *P. rufa* were heterozygous at the enzyme loci examined in this study, their unreduced spores and derivative gametes would also be heterozygous (heterozygosity at enzyme loci is common in sporophytes of sexually reproducing diploid *Pellaea* species that have been examined electrophoretically by Gastony & Gottlieb, 1985; Gastony, 1988). Fertilization involving such heterozygous gametes from different species would instantly yield an allotetraploid taxon with fixed intergenomic heterozygosity and segregating intragenomic heterozygosity. This derivation of *P. rufa* is improbable, however, because it entails the simultaneous occurrence of the same three rare events as discussed above, except that here the sporophytes producing unreduced spores would belong to different species.

A simpler explanation for the origin of the segregating intragenomic heterozygosity in *P. rufa* is based on the commonly encountered method of allotetraploid formation in ferns, chromosome doubling of an allodiploid hybrid sporophyte. An allotetraploid that arises in this way, however, should show intragenomic homozygosity and only intergenomic heterozygosity, as in the previously reported allotetraploid taxa discussed above. Only through gradual accumulation of mutations will intragenomic heterozygosity arise in such an allotetraploid taxon, and in this case different variant alleles might be expected to arise in different populations of the allotetraploid, unlike the situation in *P. rufa* where all populations examined express the same four alleles at *Pgi-2*. However, if tetraploid *P. rufa* had two or more independent origins from allodiploids with differing alleles at the various enzyme loci, as reported by Werth et al. (1985b) in *Asplenium*, random matings among the gametophytic progenies of the genetically variant allotetraploids would generate the various banding patterns of *P. rufa* sporophytes in Figures 6–8.

Rieseberg & Doyle (1989) reviewed the idea that allotetraploids may have a fitness advantage over their diploid progenitors because of the increased biochemical diversity they achieve through fixed heterozygosity resulting from the addition of two differentiated genomes. They contrasted this with an autotetraploid's ability to maintain as many as four alleles at a single locus and noted that resultant high levels of heterozygosity maintained by polysomic inheritance in autopolyploid populations are of prime importance in their evolution. *Pellaea rufa* shows that allotetraploids also can maintain as many as four alleles per locus and can generate as many isozyme variants per enzyme locus per individual (ten bands) as can autotetraploids. Meiotic segregation does generate more genetic variation from autotetraploids with four alleles per locus than from equally heterozygous allotetraploids. Nevertheless, *P. rufa* demonstrates that even disomic inheritance allows natural populations of allotetraploids to maintain higher levels of heterozygosity than has previously been reported.

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BIOSYSTEMATIC ANALYSIS OF THE *CYSTOPTERIS TENNESSEENSIS* (DRYOPTERIDACEAE) COMPLEX[1]

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ABSTRACT

The allotetraploid *Cystopteris tennesseensis* and its putative diploid progenitors, *C. bulbifera* and *C. protrusa*, constitute the *C. tennesseensis* complex. Although previous studies provided evidence of morphological, ecological, and chromosomal differences among the members of this complex, puzzling morphological variability precluded consistent identification and treatment of the taxa. The current study combined morphometric analyses with surveys of chromosomal, isozymic, and gametophytic features and supported past treatments of the complex as three separate species. The diploids shared no allozymes for the nine enzymes examined, and meiotic analyses of triploid hybrids with *C. tennesseensis* provided additional evidence that the diploid genomes are nonhomologous. Because *C. tennesseensis* has a relatively narrow range and contains isozymic profiles that are consistently additive of diploid patterns, we suggest that this allopolyploid is a relatively young species. Isozymic variation in the tetraploid parallels that observed in the diploids, implying that genetic variability was introduced through recurrent hybridization. Analyses of isozymic data and gametophytic features indicated that the diploids outcross frequently and thus may form hybrids readily when sympatric with the tetraploid. In part because of these characteristics, precise identification of species and hybrids in this complex is difficult and depends on evaluation of cryptic features.

The cosmopolitan genus *Cystopteris* Bernh. has been called "perhaps the most formidable biosystematic problem in the ferns" (Lovis, 1977, p. 356). Although *Cystopteris* species are primarily north temperate and therefore readily accessible to pteridologists, complex patterns of morphological variation have thwarted satisfactory taxonomic treatments. The most recent monograph (Blasdell, 1963) recognized ten species in two subgenera. Subgenus *Acystopteris* includes the Asian species *C. japonica* and *C. tenuisecta*, which are so distinctive that some have placed them in a separate genus (Nakai, 1933; Pichi-Sermolli, 1977). Blasdell divided the remaining species (all in subg. *Cystopteris*) into two sections based on the pattern of vein termination in the leaves. Species having veins directed into teeth were placed in sect. *Cystopteris*, while those with veins directed into sinuses were assigned to sect. *Emarginatae*. Blasdell encountered variability for this vein termination character in some specimens and suggested that such anomalies could result from introgression. Lovis (1977), on the other hand, considered it more likely that venation features are not as stable in some species as in others and should not be used to define sections.

Our observations suggested that Lovis was correct and, rather than organizing the North American *Cystopteris* species into morphologically based sections, we have chosen to concentrate on interactive species complexes involving allopolyploid species and their putative diploid progenitors. One

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such complex centers on *C. tennesseensis*, a species first recognized by Shaver (1950) who described it as a hybrid between *C. bulbifera* and *C. protrusa*. In 1954 Shaver developed an extended discussion of the morphology and ecology of the complex which still stands as an excellent summary of the natural history of this difficult group.

From the moment it was named, there was disagreement concerning the proper status and disposition of *C. tennesseensis*. McGregor (1950), in collaboration with C. A. Weatherby, reduced this species to a variety of *C. fragilis*. In addition, citing specimens that did not conform to the protologue of *C. fragilis* var. *tennesseensis* and that seemed to be close to Weatherby's *C. fragilis* f. *simulans*, McGregor recognized *C. fragilis* var. *simulans*. This approach seemed justified because some specimens tend to bridge the morphological gap between these two varieties as well as between *C. fragilis* var. *fragilis* and *C. fragilis* var. *tennesseensis*. However, Blasdell (1963) revealed *C. tennesseensis* as a tetraploid with $n = 84$ chromosomes. His analysis showed that hybridization between *C. protrusa* and *C. bulbifera* was the most reasonable explanation for the origin of this tetraploid. Therefore, Blasdell resurrected *C. tennesseensis* as a species, including the former *C. fragilis* var. *simulans*.

The subtlety of morphological features separating the species as well as the continued discovery of intermediates has perpetuated the systematic confusion of the *C. tennesseensis* complex. Even though the accumulated data demonstrate conclusively that *C. tennesseensis* is isolated from its congeners, this tetraploid has not been widely accepted as a distinct species. As recently as 1982, Moran (1982, p. 94) found in a study of *Cystopteris* specimens from Illinois that "all 90 herbarium specimens of *C. tennesseensis* . . . were originally misidentified."

In this paper, we report a series of analyses designed to investigate the patterns and the processes behind the systematic confusion in *C. tennesseensis*. We describe studies of biogeography, morphology, chromosomes, and isozymes that clarify the origin and current status of *C. tennesseensis* and its progenitor diploids.

Materials and Methods

Observations of morphological variability, geographic distribution, and habitat diversity were obtained from surveys of herbarium specimens. If specific locality data were supplied, collection sites were plotted by county and used to obtain distributional information. When the gross morphology of specimens was not sufficient to assign them readily to species, spores were removed and mounted in Permount on glass microscope slides. The longest diameter of the monolete spores (Table 1) and evidence of abortion (e.g., shrunken or malformed spores) was noted. Spore slides were placed in envelopes and attached to herbarium sheets.

To supplement herbarium collections and supply living material for chromosomal, isozymic, and common garden morphological comparisons, specimens were collected over much of the range of the genus in North America and were donated as noted in footnote 1. Living collections were maintained in the University of Kansas greenhouses. Collection sites for materials used in this study are listed in Table 2.

Ecologically induced morphological variation may obscure genetically based species distinctions. Therefore, we conducted discriminant analyses of morphological variation based on plants cultivated in the greenhouse. All individual plants were identified and assigned to a group on the basis of chromosome number and isozymic composition. Fea-

Table 1. Mean spore sizes and standard deviations calculated by measuring the long axis of 25 spores. Specimens whose ploidy level has been verified by meiotic chromosome squashes are indicated by asterisks. States listed in parentheses are those from which the specimens were collected.

C. bulbifera (Illinois)	37.48 ± 1.949
*C. bulbifera** (Oklahoma)	35.21 ± 3.408
*C. bulbifera** (Arizona)	36.27 ± 2.560
*C. bulbifera** (Indiana)	35.96 ± 2.325
*C. bulbifera** (Ohio)	39.81 ± 2.944
C. bulbifera (Ohio)	35.71 ± 3.038
C. bulbifera (Kentucky)	34.39 ± 1.764
C. bulbifera (Indiana)	36.78 ± 2.336
	mean = 36.45 ± 1.650
C. protrusa (Illinois)	33.65 ± 1.788
*C. protrusa** (Kansas)	35.22 ± 4.714
C. protrusa (Missouri)	33.33 ± 2.421
*C. protrusa** (Kansas)	30.77 ± 1.868
*C. protrusa** (Kansas)	30.98 ± 2.260
*C. protrusa** (Michigan)	33.21 ± 2.332
*C. protrusa** (North Carolina)	34.22 ± 3.042
	mean = 33.05 ± 1.634
*C. tennesseensis** (Kansas)	40.02 ± 3.250
*C. tennesseensis** (Missouri)	41.40 ± 1.907
*C. tennesseensis** (Illinois)	41.29 ± 2.416
*C. tennesseensis** (Arkansas)	40.65 ± 2.084
	mean = 40.84 ± 0.639

TABLE 2. Locality data for collections providing material for electrophoretic and cytogenetic analyses. Asterisks indicate localities used for population genetic analyses (see Table 4).

Locality	Collector	Chromosome number verified?
Cystopteris bulbifera		
Arizona: Coconino Co., Rio de Flag	*Windham 194*	Yes, 42II
Arizona: Coconino Co., Oak Creek Canyon	*Windham 314*	Yes, 42II
Arizona: Coconino Co., Lower West Fork	*W. H. Wagner 82113*	Yes, 42II
Indiana: Fountain Co., Portland Arch*	*C. H. Haufler & R. C. Moran s.n.*	No
Indiana: Jefferson Co., Clifty Falls	*C. H. Haufler & R. C. Moran s.n.*	No
Indiana: Monroe Co., Cedar Bluffs*	*C. H. Haufler & R. C. Moran s.n.*	No
Kentucky: Powell Co., Natural Bridge*	*C. H. Haufler & R. C. Moran s.n.*	No
Ohio: Adams Co., near Stout*	*C. H. Haufler & R. C. Moran s.n.*	Yes, 42II
Oklahoma: Ottawa Co., Dripping Springs	*C. H. Haufler & C. K. Teale s.n.*	Yes, 42II
Wisconsin: Door Co., Peninsula State Park	*W. C. Taylor s.n.*	Yes, 42II
C. protrusa		
Iowa: Fremont Co., SW of Sidney	*R. E. Brooks 14929*	Yes, 42II
Illinois: Cook Co., McGinness Slough Conservation Area	*R. C. Moran s.n.*	No
Illinois: Union Co., Shawnee National Forest	*C. H. Haufler s.n.*	Yes, 42II
Indiana: Monroe Co., Cedar Bluffs*	*C. H. Haufler & R. C. Moran s.n.*	No
Indiana: Monroe Co. Cascades Park*	*C. H. Haufler s.n.*	No
Indiana: Monroe Co., Farr Road*	*C. H. Haufler & R. C. Moran s.n.*	No
Indiana: Perry Co., N of Tell City*	*C. H. Haufler s.n.*	No
Kansas: Douglas Co., Breidenthal Woods*	*Windham 579*	Yes, 42II
Kansas: Chautauqua Co., W of Elgin	*R. E. Brooks 16162*	Yes, 42II
Kansas: Miami Co., S of Homewood	*C. H. Haufler s.n.*	Yes, 42II
Michigan: Washtenaw Co., Homer Woods	*C. H. Haufler & W. H. Wagner s.n.*	Yes, 42II
Missouri: Boone Co., SW of Columbia	*R. E. Brooks 15298*	Yes, 42II
Missouri: Cooper Co., Arrow Rock	*R. E. Brooks & C. H. Haufler 15343*	Yes, 42II
Missouri: Franklin Co., Meramec State Park	*R. E. Brooks & C. H. Haufler 15341*	Yes, 42II
Missouri: St. Louis Co., near Allenton*	*R. E. Brooks & C. H. Haufler 15332*	Yes, 42II
North Carolina: Swain Co., Nantahala Gorge	*W. H. Wagner s.n.*	Yes, 42II
C. tennesseensis		
Illinois: Jackson Co., Fountain Bluff	*C. H. Haufler & R. C. Moran s.n.*	Yes, 84II
Kansas: Doniphan Co., N of Wathena	*R. E. Brooks 14898*	Yes, 84II
Missouri: Franklin Co., E of Sullivan	*R. E. Brooks & C. H. Haufler 15334*	Yes, 84II
Missouri: LaClede Co., Big Niangua River	*B. C. Phillips s.n.*	Yes, 84II
Nebraska: Richardson Co., NE of Shubert	*R. E. Brooks 14925*	Yes, 84II
Oklahoma: Ottawa Co., Dripping Springs	*C. H. Haufler & C. K. Teale s.n.*	Yes, 84II
C. tennesseensis × *C. bulbifera*		
Missouri: Boone Co., SW of Columbia	*R. E. Brooks & C. H. Haufler 15302*	Yes, 42II + 42I
Nebraska: Richardson Co., NE of Shubert	*R. E. Brooks 14925a*	Yes, 42II + 42I
C. tennesseensis × *C. protrusa*		
Kansas: Chautauqua Co., W of Elgin	*R. E. Brooks 16163*	Yes, 42II + 42I
Missouri: St. Louis Co., near Allenton	*R. E. Brooks & C. H. Haufler 15331*	Yes, 42II + 42I

tures surveyed are listed in Table 3 and depicted in Figure 1. Because the species are often difficult to discern based solely on leaf features (often the only part preserved on herbarium specimens), we first used only quantitative leaf features to seek species-specific leaf attributes or combinations thereof. Involved in this analysis were 9 plants of *C. bulbifera*, 21 of *C. protrusa*, and 8 of *C. tennesseensis*. Because our first analysis could not completely discriminate the species (see Results),

a second analysis was conducted that included qualitative characters (Table 3) as well as mean spore sizes per plant (Table 1). This second analysis included 8 plants of *C. bulbifera*, 14 of *C. protrusa*, and 4 of *C. tennesseensis*. The data from both sets were analyzed with the BMDP7M stepwise discriminant analysis program (BMDP Statistical Software, 1981, UC Press). For each step in the analyses we allowed an experiment-wise error rate of $\alpha = 0.05$ and judged the significance of each approximate F-ratio as the criterion for entry of a variable into the discriminant models. The critical values of F were estimated using Bonferroni's inequality (Ranker & Schnabel, 1986).

Unlike angiosperms, the gametophyte generation of fern species is independent of the sporophyte. Whereas the sporophyte is important in maintaining long-term survival of individuals, the gametophyte carries out sexual reproduction and initial establishment of populations. Thus, in developing a complete picture of the biology of fern species as well as characterizing evolutionary tendencies, analyses of gametophyte reproductive biology are necessary. In a previous study Haufler & Ranker (1985) determined which *Cystopteris* species produced and/or responded to antheridiogen. In the present study 100 gametophytes of each species were reared individually, employing the culture conditions described in Haufler & Ranker (1985), and assayed for genetic load following the procedures outlined by Lloyd (1974).

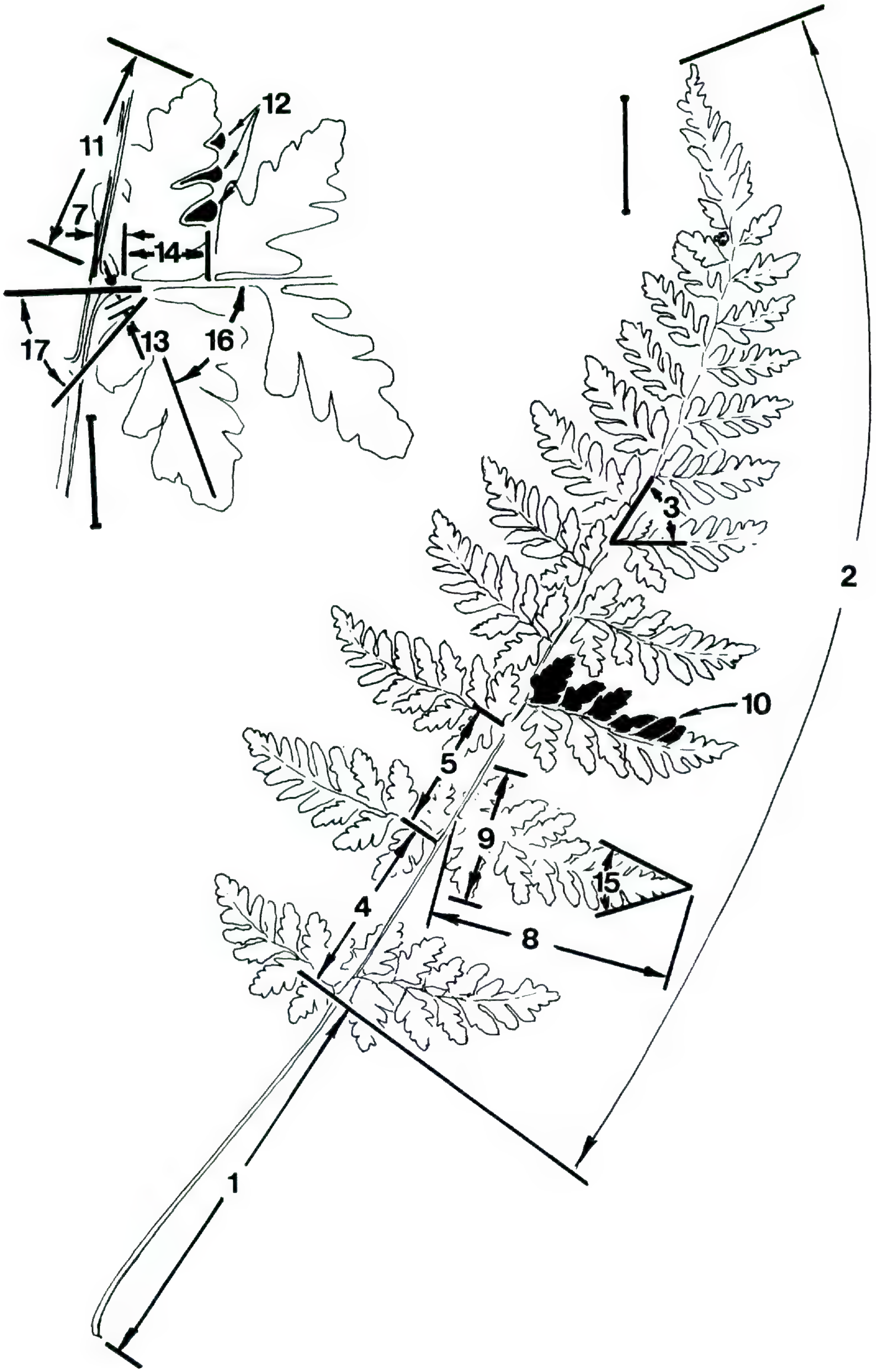
Analyses of chromosomal behavior at meiosis were especially important in characterizing suspected hybrid individuals. The procedures followed in obtaining and photographically documenting stages in sporogenesis were described in Haufler et al. (1985). Voucher specimens for each chromosome count will be deposited at KANU.

Electrophoretic analyses of isozyme variability were performed as described by Haufler (1985). Leaf samples were ground in the phosphate grinding buffer of Soltis et al. (1983) using a mortar and pestle or by placing them in spot plate wells and using a round-bottomed centrifuge tube as a pestle. Each of the 22 enzymes listed in Soltis et al. (1983) was surveyed and was subjected to a variety of gel and electrode buffer conditions (largely those of Soltis et al., 1983). Enzymes that provided consistent, interpretable results were hexokinase (HK), isocitrate dehydrogenase (IDH), leucine amino peptidase (LAP), the more cathodal (presumably cytosolic—see Weeden, 1983) bands of phosphoglucoisomerase (PGI-2), two sets of bands (presumably representing cytosolic and chloroplastic enzymes—see Weeden, 1983) for phosphoglucomutase (PGM-1, the more anodal set, and PGM-2, the more cathodal set), shikimate dehydrogenase (SkDH), and two sets of bands (presumably representing cytosolic and chloroplastic enzymes—see Weeden, 1983) for triosephosphate isomerase (TPI-1, the more anodal set, and TPI-2, the more cathodal set). HK, PGI-2, LAP, TPI-1, and TPI-2 showed the best resolution on either system 6 of Soltis et al. (1983) or the modified system 8 discussed in Haufler (1985). IDH, PGM-1, PGM-2, and SkDH were resolved best on the modified system 11 of Soltis et al. (1983) discussed in Haufler (1985). Identification of bands shared among populations and species was accomplished through coelectrophoresis of the samples on the same gel.

Individual gametophytic progeny were used to assess the genetics of sporophytic banding patterns. We followed the electrophoretic procedures de-

TABLE 3. List of features included in morphometric analysis. Asterisks indicate those illustrated in Figure 1. Plus marks indicate features that were statistically significant in discriminating species.

1–5.	FEATURES OF ENTIRE LEAF
*1.	Length of petiole (cm)
*2.	Length of blade (cm)
*3.	Angle of departure of median pinna
*4.	Length of rachis between lowest pinna of first pinna pair and lowest pinna of second pinna pair (mm)
*5.	Length of rachis between lowest pinna of second pinna pair and lowest pinna of third pinna pair (mm)
6–17.	FEATURES OF LONGEST PINNA
6.	Number of pinna pairs from base (first one = number 1)
*7.	Length of pinna stalk (petiolule) (mm)
*8.	Length of pinna (mm)
*9.	Width of pinna (mm)
+*10.	Number of segments along acroscopic edge of pinna (including pinnatifid ones)
*11.	Length of first acroscopic pinnule (mm)
*12.	Number of major sinuses along distal edge of first acroscopic pinnule
*13.	Length of stalk of basiscopic pinnule (mm)
*14.	Length of pinna rachis between lowest two pinnule pairs (mm)
*15.	Angle formed by apex of pinna
+*16.	Angle formed by basiscopic pinnule axis with pinna axis
*17.	Angle of proximal portion of basiscopic pinnule base with pinnule axis
18–20.	QUALITATIVE FEATURES
18.	Presence or absence of bulblets
+19.	Presence or absence of glandular trichomes
20.	Color of petiole
+21.	Spore size (see Table 1)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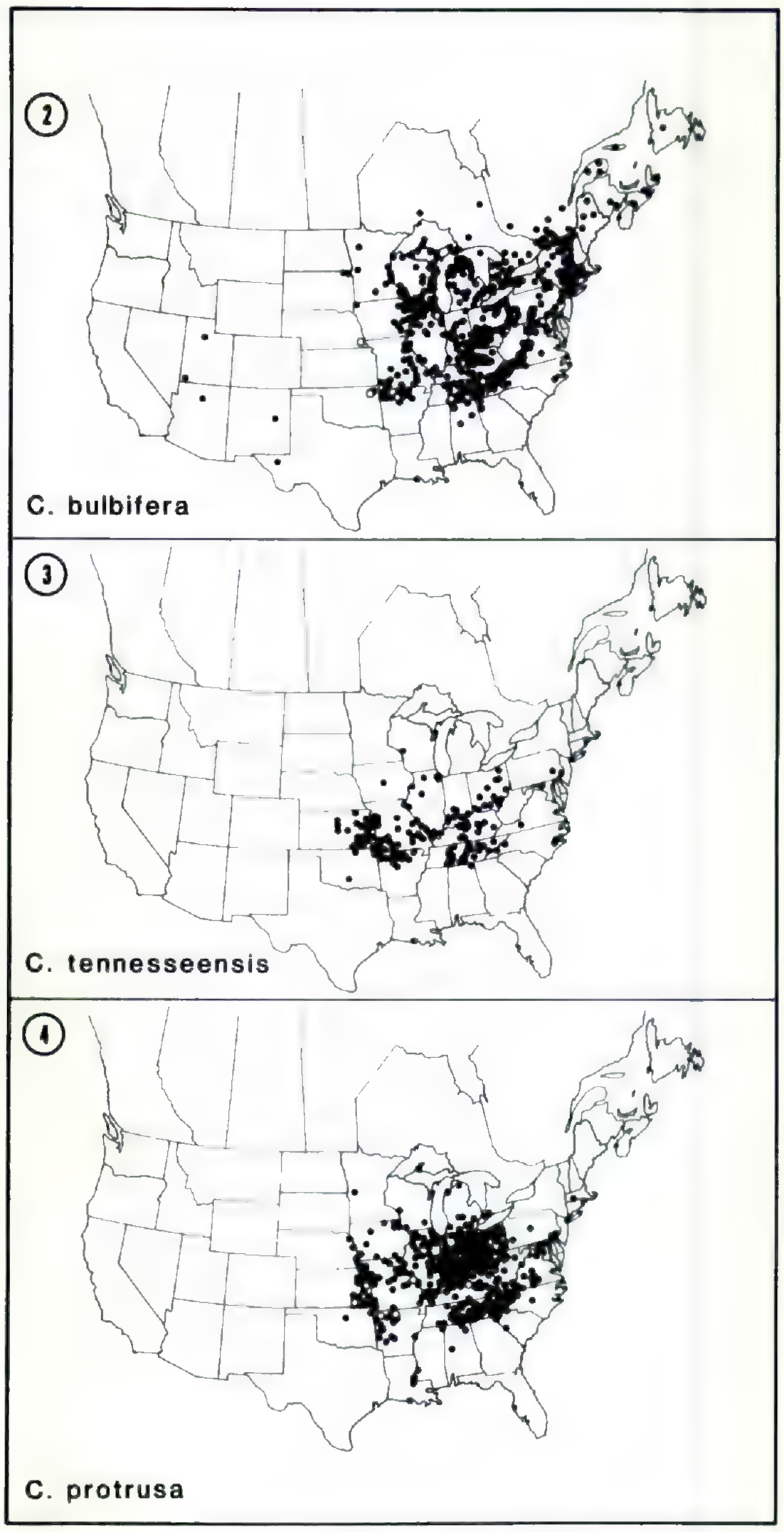
scribed by Gastony & Gottlieb (1982) as modified by Haufler & Soltis (1984). For the enzymes surveyed, gametophytes express the same isozymes as do sporophytes. Because gametophytes are multicellular, haploid individuals derived from single meiotic products (spores), gametophytic progeny arrays from single sporophytes can be used to determine directly the genetic constitution of complex sporophytic banding patterns. In this way, segregational analyses of putatively heterozygous banding patterns can be performed without pursuing more time-consuming crossing programs.

After allelic determinations were made for each of the nine putative loci, allozymic data from a set of representative populations (Table 4) were analyzed. The proportion of polymorphic loci (P) and the mean number of alleles per locus (A) were calculated from these populational data. A statistical program (LYNSPROG) written by Marilyn Loveless, The College of Wooster, Wooster, Ohio, was used to calculate levels of heterozygosity, the fixation index (F), and Nei's coefficients of genetic identity and distance. Because *C. protrusa* tends to be clonal, separate calculations were made for populations consisting of (1) each leaf sampled (ramets) and (2) only the number of different genotypes (genets). The first should overestimate the number of individual organisms while the second should underestimate it.

Results

Spores

Blasdell (1963) and Moran (1982) noted the value of spore features for identifying hybrids and in determining the ploidy of specimens. Despite Lovis's (1977) caveat that it may not be appropriate in *Cystopteris* to infer ploidy levels from spore measurements, we were able to verify independently through analyses of meiotic chromosome behavior that spore size did correlate with several critical genetic features of species (Table 1). We agree with Lovis that spore size comparisons alone do not substitute for direct chromosome analyses, but once a strong correlation between spore features and genetic condition is established, spores can be extremely valuable in surveying specimens rapidly. Each species differed significantly in mean spore size from the other two (pairwise t-tests, $P < 0.002$). Although *C. bulbifera* spores were larger than those of *C. protrusa*, spores of tetraploid *C. tennesseensis* showed the further size increase commonly associated with higher ploidy.



FIGURES 2–4. Geographic distributions of members of the *Cystopteris tennesseensis* complex based on data from herbarium specimens. Dots indicate counties where specimens were collected.—2. *C. bulbifera*.—3. *C. tennesseensis*.—4. *C. protrusa*. Open circles on Figures 2 and 4 show locations of putative triploid backcross hybrids.

Morphological analyses of sporophytes

The taxa in the *Cystopteris tennesseensis* complex are among the most distinctive in the genus. There are more unique features that characterize

←

FIGURE 1. Leaf features included in morphometric analysis. Numbers correspond to descriptions of features in Table 3. Scale bars: for whole leaf = 2.0 cm; for pinna base = 0.5 cm.

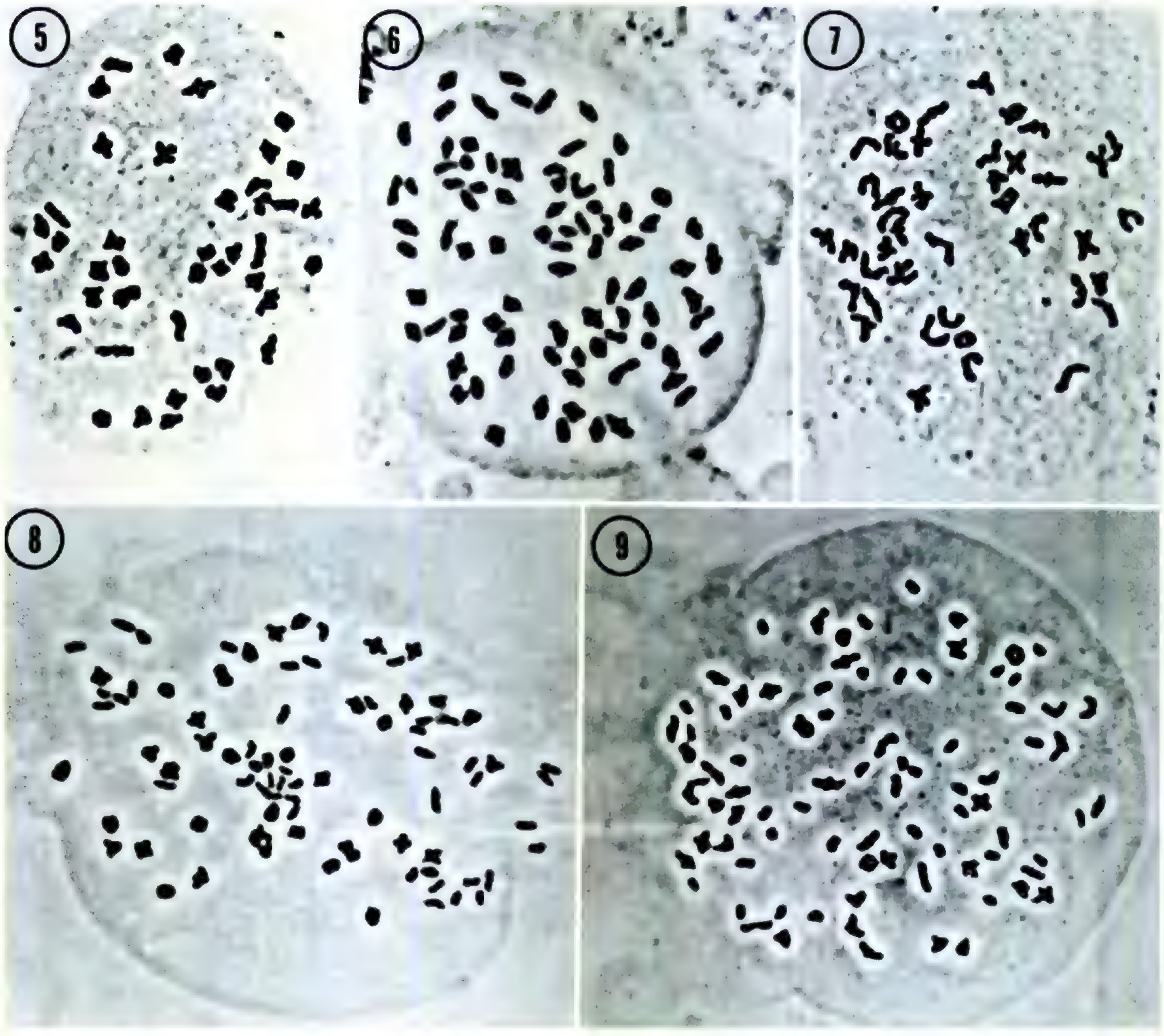
each species than there are in any other group of *Cystopteris* species. *Cystopteris protrusa*, for example, has long internodes and a peculiar, protruding rhizome apex whose growing point extends past the current season's leaves. Given the evidently rapid growth of the rhizome, we were not surprised to find extensive clones of this species in mature woodlands. *Cystopteris bulbifera*, commonly found on moist cliffs, has short internodes and bears asexual reproductive bulblets on its leaves, and most individuals have tack-shaped, glandular trichomes that are particularly prominent on the indusia and along the rachis between pinnae. The allotetraploid *C. tennesseensis* combines the genomes of its progenitor diploids and, perhaps as a result of this genetic amalgamation, is morphologically variable. In many features, the tetraploid is intermediate between the diploids, e.g., it has poorly formed bulblets and a reduced frequency of glandular trichomes. Its rhizome features, however, are not intermediate. Perhaps because it inhabits somewhat disturbed, often dry cliffs rather than forest floors, it has the short internodes typical of *C. bulbifera*.

Even though past workers (Shaver, 1954; Blasdell, 1963) provided well constructed species descriptions and indicated the distinctive features of each species, taxonomists not familiar with the genus continue to encounter problems when identifying members of the *C. tennesseensis* complex. To generate additional discriminating features and in trying to separate environmentally induced variability from that based on genetic differences, we performed a discriminant analysis of leaf morphology on plants grown in a common garden. In the first analysis, employing only quantitative leaf characters, only two features were entered into the model as being statistically significant, the number of acroscopic segments on the longest pinna (#10, Table 3, Fig. 1) and the angle formed by the basiscopic pinnule axis with the pinna axis (#16). The species differed significantly from one another in the space defined by the two canonical axes ($P < 0.01$). The first axis accounted for 85% of the total variance and separated *C. bulbifera* from the other two species. The two variables in the model exhibited similar character loadings (standardized coefficients) on the first axis, 0.608 for #10 and 0.720 for #16, indicating a nearly equal contribution to the canonical variable. Inspection of the original data revealed that *C. bulbifera* is distinguished from the other species by a larger number of acroscopic segments on the longest pinna and a larger angle formed by the basiscopic pinnule. The second axis accounted for the remaining 15% of the variance. The jackknifed classification matrix correctly identified 100% of the *C. bulbifera* individuals, 71.4% of *C. protrusa*, and 87.5% of *C. tennesseensis*. Six individuals of *C. protrusa* were incorrectly identified as *C. tennesseensis*, and one individual of *C. tennesseensis* was incorrectly identified as *C. protrusa*.

A second discriminant analysis was conducted in which qualitative leaf features (listed in Table 3) and spore size were added to the data set in an attempt to identify combinations of characters that would allow a better discrimination of species than was obtained in the first analysis. In this second analysis, three characters were entered into the model as statistically significant: angle of the basiscopic pinnule (#16), presence or absence of glandular trichomes, and mean spore size (Table 1). The first canonical axis accounted for 82% of the total variance, and the character loadings were 0.809 (#16), 0.875 (glandular trichomes), and 0.485 (spore size). The first axis primarily separated the two diploids from one another. As indicated by the relative value of the loadings, the diploids were primarily distinguished by the angle of the basiscopic pinnule and the presence or absence of glandular trichomes. On the second axis, the character loadings were −0.081 (#16), 0.429 (glandular trichomes), and −0.887 (spore size). The large spore size of the tetraploid, therefore, was the most important factor in discriminating it from the diploids. The jackknifed classification matrix produced 100% correct classifications for all individuals in the analysis.

BIOGEOGRAPHY

The distribution of species is shown in Figures 2–4. *Cystopteris bulbifera* is the most northern species, extending well into Canada. *Cystopteris protrusa* is most common in the east-central United States and is rare in southern Canada (Britton et al., 1984; Haufler et al., 1985). The allotetraploid derivative *C. tennesseensis* is found primarily in the region of overlap of the two diploids. Using spore abortion as an indicator of sterility, we identified interspecific hybrids between the tetraploid and its diploid parents. The locations of these hybrids are indicated as open circles on Figures 2 and 4. Because the morphological features are quite plastic, it is not always possible to determine which of the diploids hybridized with *C. tennesseensis* in forming the sterile plants. Using chromosomal and isozymic data, we were able to document that backcrosses to both parents do occur in nature (see below).

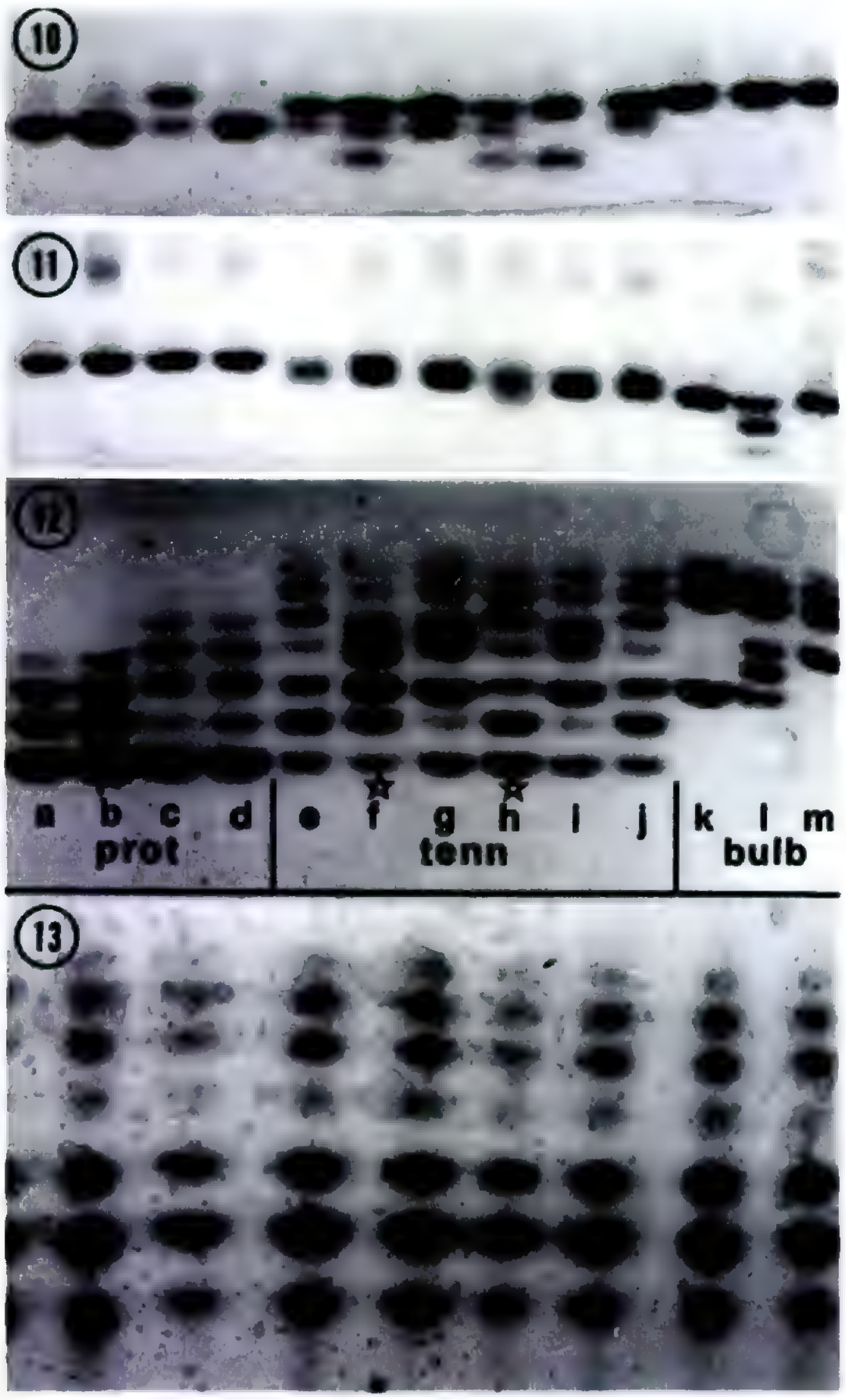


FIGURES 5–9. Representative meiotic chromosome squashes.—5. *C. bulbifera*, $n = 42II$.—6. *C. tennesseensis*, $n = 84II$.—7. *C. protrusa*, $n = 42II$. 8, 9. Backcross hybrids between *C. tennesseensis* and its diploid progenitors. Identification of hybrids was based on morphological and isozymic data.—8. Hybrid between *C. tennesseensis* and *C. bulbifera*, $n = 42II + 42I$.—9. Hybrid between *C. tennesseensis* and *C. protrusa*, $n = 42II + 42I$. All × 1,000.

GAMETOPHYTES

Summarizing previous studies of *Cystopteris* gametophytes (Blasdell, 1963; Profumo, 1969; Auquière & Moens, 1972), Blasdell (1963, p. 6) stated, "All of the taxa examined are similar in the bulk of their gametophytic features." Our study of gametophyte ontogeny confirmed Blasdell's assessment of the level of morphological variability. However, Haufler & Ranker (1985) demonstrated significant interspecific variation in response to the pheromone antheridiogen.

Genetic load studies have been used to look into aspects of reproductive biology (Lloyd, 1974). Because inbreeding brings about the expression of recessive alleles, species with low genetic load should be more inbred, whereas those having high genetic load are presumed to be outcrossers. In homosporous ferns, levels of genetic load can be determined by assessing the ability of isolated gametophytes to produce sporophytes. In the present study, none of the 100 isolated gametophytes of *C. bulbifera* and *C. protrusa* produced sporophytes, even after repeated waterings over a four-month period. However, 25 of the 100 isolated gametophytes of *C. tennesseensis* did form sporophytes. Although we did not examine each isolated gametophyte, we have verified that gametophytes of the diploid species do become hermaphroditic in culture. Thus, genetic load in the tetraploid is significantly lower than that in the diploids (3×2 contingency table of species vs. sporophyte production: $G = 59.63$, $P < 0.001$).



FIGURES 10–13. Representative isozyme profiles. Anode = top of photographs, cathode = bottom of photographs. 10–12. Interspecific comparisons of banding patterns. Lanes a–d = *C. protrusa*; e–j = *C. tennesseensis*; k–m = *C. bulbifera*. Lanes f and h (starred) are from triploid backcross hybrids between *C. tennesseensis* and *C. protrusa*.—10. SkDH (monomeric, single compartment). Compare lanes i and j where the upper band of these fixed heterozygotes are from *C. bulbifera* and the lower bands are from *C. protrusa*. Differences in the *C. protrusa* contribution may have resulted from recurring origin of the tetraploid. Note that the backcross hybrids contain both *C. protrusa* bands.—11. PGI (dimeric; anodal, presumably chloroplastic bands are not well resolved and were not scored; cathodal bands are presumably cytoplasmic). Because the *C. bulbifera* and *C. protrusa* bands have very similar mobilities, the fixed heterozygous pattern in *C. tennesseensis* appears as a broad fuzzy band consisting of the parental bands and an interlocus heterodimeric band.—12. TPI (dimeric; in both diploids, anodal, multiple-banded pattern probably represents a post-translational modification of the enzyme (see discussion in Gastony, 1988, and Hickey et al., 1989)); cathodal bands show typical dimeric enzyme expression in homozygotes and heterozygotes (compare lanes k–m); in tetraploids, anodal and cathodal bands overlap. Lanes a and b vs. lanes c and d show differing mobilities for the multiple-banded enzymes. Lanes i and j probably are from plants that had different *C. bulbifera* parents. Lane i received the more anodal band from *C. bulbifera* while lane j received the more cathodal band.—13. TPI expression in individual gametophytic progeny of a sporophyte having the banding pattern seen in lanes e and j of Figure 12. There is no segregation for the complex pattern, indicating that the sporophyte was a fixed heterozygote.

MEIOTIC CHROMOSOME BEHAVIOR

Analyses of meiosis from plants collected across the species ranges generated consistent counts of $n = 42$ in *C. bulbifera* (Fig. 5) and *C. protrusa* (Fig. 7), and $n = 84$ in *C. tennesseensis* (Fig. 6). Table 2 lists the collection localities of the plants yielding new chromosome counts. In addition to analysis of the sexual species, plants verified via isozyme analysis to be backcross hybrids were also studied cytogenetically. As shown in Figures 8 and 9, all hybrids showed a complement of 42 bivalents plus 42 univalents expected from backcross hybrids of an allotetraploid to its diploid progenitors. These results indicate little or no chromosomal homology between the diploid species *C. protrusa* and *C. bulbifera* and suggest that *C. tennesseensis* contains one genome of each.

ISOZYMES

Isozyme patterns of the tetraploid *C. tennesseensis* are perfectly additive of those from the two diploid species. Gametophytic progeny arrays demonstrated that the complex banding patterns did not segregate during meiosis (Fig. 13), suggesting that the isozymes comprising these patterns were coded by genes situated on nonhomologous chromosomes contributed by the two diploid parents. Given that all tetraploids showed fixed heterozygosity that always combined patterns from each diploid progenitor, no evidence of "orphan alleles" or gene silencing could be detected. All isozymic variability observed in the allotetraploid apparently resulted from the incorporation of various diploid allozymes into the polyploid derivative via recurring allopolyploid events (Figs. 10–12, and see Haufler & Soltis, 1986).

Combining chromosomal and isozymic data made it possible to identify hybrids and determine their parentage. Sporogenesis was studied in plants having aborted spores. Such plants were shown to be triploids having 42 pairs and 42 univalents during meiosis and thus were determined as backcrosses between *C. tennesseensis* and either *C. protrusa* or *C. bulbifera*. Even though the variability of morphological features could preclude precise identification of parents, the triploids always contained unequal enzyme contributions from the two parents. Thus, dosage effects could be used to show

TABLE 4. Locations and sizes (n) of populations of diploid *Cystopteris* species surveyed in generating genetics statistics (see Tables 5–7).

Cystopteris bulbifera

Population #1—Fountain Co., Indiana, Portland Arch, N of Covington—$n = 18$
Population #2—Adams Co., Ohio, limestone cliffs near Stout—$n = 41$
Population #3—Monroe Co., Indiana, Cedar Bluffs, S of Bloomington—$n = 11$
Population #4—Powell Co., Kentucky, along trail in Natural Bridge State Park—$n = 12$

C. protrusa

Population #1—Douglas Co., Kansas, Breidenthal Woods, near Lawrence
Population #2—Monroe Co., Indiana, Cedar Bluffs, S of Bloomington
Population #3—Monroe Co., Indiana, Cascades Park, NNW of Bloomington
Population #4—Monroe Co., Indiana, Farr Rd., N of Bloomington
Population #5—St. Louis Co., Missouri, near Allenton
Population #6—Perry Co., Indiana, N of Tell City

Population sizes for *C. protrusa* calculations

First set of calculations based on ramets	Second set of calculations based on genets
Population #1—$n = 104$	Population #1—$n = 15$
Population #2—$n = 17$	Population #2—$n = 3$
Population #3—$n = 18$	Population #3—$n = 2$
Population #4—$n = 12$	Population #4—$n = 6$
Population #5—$n = 10$	Population #5—$n = 7$
Population #6—$n = 24$	Population #6—$n = 10$

which backcross had formed the hybrids. Hybrids formed between *C. tennesseensis* and *C. protrusa* had the *C. protrusa* bands stained more intensely than the *C. bulbifera* contribution (Figs. 10–12, lanes f and h). Conversely, *C. tennesseensis* × *C. bulbifera* hybrids contained a double dose of *C. bulbifera*.

Although all nine enzymes helped corroborate that *C. tennesseensis* was an amalgam of its progenitor diploids, the most complex and informative enzyme was TPI (Fig. 12). For both diploids, banding patterns indicative of two genetic loci were resolved. The cathodal bands showed banding patterns typical of dimeric enzymes (single-banded in homozygotes and three-banded in heterozygotes). The anodal zone of bands were expressed as fixed, multiple-banded patterns which probably represent post-translational modifications (Gastony, 1988; Hickey et al., 1989). In *C. protrusa* (lanes a–d), the strongly staining, most cathodal band was an invariant marker for the species. The more weakly staining, multiple-band pattern was variable. As shown in Haufler & Soltis (1986), three patterns were detected among the sporophytes surveyed: a slow-migrating triplet (as in lanes a and b of the present paper), a fast-migrating triplet (not illustrated here, but see Haufler & Soltis (1986, fig. 1a)), and the complex, five-banded heterozygote between them (as in lanes c and d). In *C. bulbifera* (lanes k–m), the rapidly migrating triplet pattern was invariant while there were two alleles expressed for the cathodal locus. Lane l is the heterozygote formed from outcrossing between homozygotes such as k and m. When these diploid variants are combined in *C. tennesseensis* (lanes e–j), some remarkably complex patterns result. Lanes e and j appear to be relatively simple additive patterns between plants such as those in lanes a (*C. protrusa*) and k (*C. bulbifera*). Lanes g and i combine the bands found in lanes a and m. Lane f (identified via morphology and meiotic chromosomal behavior as a triploid backcross between *C. protrusa* and *C. tennesseensis*) combines one dose of a profile like lane m with two doses of lane b. Lane h (also a *C. protrusa* × *C. tennesseensis* triploid) appears to combine one dose of a plant like lane k with two doses of one like lane b or c. Note also the banding patterns for the triploids in SkDH (Fig. 10). For lanes f and h, the two cathodal bands are shared with *C. protrusa* while only the most anodal band is found in *C. bulbifera*. These SkDH patterns help confirm that both triploids contain two genomes from *C. protrusa* and only one from *C. bulbifera*. The slowest migrating SkDH band in *C. tennesseensis* (lanes f, h, and i) is from *C. protrusa* even though it is not seen in the representative *C. protrusa* plants on this gel. The rapidly migrating SkDH band in lane c is a rare *C. protrusa* variant

TABLE 5. Population genetics statistics. P = proportion polymorphic loci, A = average number of alleles per locus. P and A were identical for the ramet and genet samples of *C. protrusa*.

Cystopteris bulbifera

Population number	P	A	Mean heterozygosity Observed	Mean heterozygosity Expected
1	0.67	1.89	0.435	0.470
2	0.56	1.78	0.138	0.219
3	0.56	1.78	0.394	0.334
4	0.67	1.78	0.347	0.273
Mean	0.62	1.81	0.329	0.324

Cystopteris protrusa

Population number	P	A	Mean heterozygosity for ramets Observed	Mean heterozygosity for ramets Expected	Mean heterozygosity for genets Observed	Mean heterozygosity for genets Expected
1	0.56	1.67	0.128	0.153	0.152	0.223
2	0.22	1.22	0.042	0.104	0.048	0.134
3	0.56	1.56	0.524	0.302	0.429	0.286
4	0.78	1.88	0.357	0.342	0.286	0.345
5	0.56	1.67	0.157	0.235	0.204	0.273
6	0.44	1.56	0.185	0.176	0.200	0.198
Mean	0.52	1.59	0.232	0.219	0.220	0.243

not incorporated in any of the *C. tennesseensis* plants shown here.

A series of populations was surveyed (Table 4) and used to generate calculations of P, A, and levels of heterozygosity (Table 5), Nei's coefficients of genetic identity and distance (Table 6), and the fixation index (*F*) (Table 7). Results derived from ramet and genet views of individuality in populations of *C. protrusa* did not differ markedly. Observed heterozygosity differed by 0.012 and mean genetic identities were within 0.013 of each other. Although the calculations of *F* derived from the ramet samples appear to have a large number of significant departures from random mating, these values are both positive and negative. A mean of −0.0687 for these significant values suggests that the ramet figures may be influenced by oversampling of certain clonal genotypes. *Cystopteris bulbifera* and *C. protrusa* shared no alleles at the loci examined; thus, based on nine putative loci (most of which code for "conservative" enzymes (Gillespie & Kojima, 1968)), the genetic identity between these congeneric species was zero.

DISCUSSION

BIOGEOGRAPHY AND ECOLOGY

Fieldwork and mapping of species distributions provided new perspectives on the biology and evolution of the *Cystopteris tennesseensis* species complex. Often two and occasionally all three species were sympatric. In such situations, *C. protrusa* was confined to the forest floor, *C. bulbifera* was on moist cliffs and among the talus at the base of cliffs, and *C. tennesseensis* could be found on drier cliffs and/or disturbed sites such as old rock walls. When plants of *C. protrusa* and *C. bulbifera* were intermingled, a special effort was made to locate the primary diploid hybrid between them. However, primary hybrids could not be found. Others have noted that primary hybrids of well established allopolyploids can rarely be discovered (e.g., the Appalachian *Asplenium* complex (Wagner, 1954; Werth et al., 1985a) and the *Dryopteris carthusiana* complex (Wagner, 1971)). Perhaps in these situations, the intermediate niche necessary for establishment of a diploid hybrid is occupied by the allopolyploid species.

In contrast to the primary diploid hybrid situation, when *C. tennesseensis* was sympatric with either parent, triploid backcross hybrids could be identified. Although an equivalent number of stations having putative hybrids has been identified (Figs. 2, 4), fieldwork demonstrated that at any one locality, hybrids with *C. protrusa* were more frequent than those involving *C. bulbifera*. This result may reflect the greater specificity of gametophytic safe sites for the latter species. Alternatively, differences in hybrid frequencies could be related to variation in response to antheridiogen. Haufler & Ranker (1985) showed that *C. protrusa* responded to antheridiogen while *C. bulbifera* did not, and that *C. tennesseensis* had a reduced sensitivity to this antheridia-inducing pheromone. Under these circumstances, it is likely that crosses involving *C. protrusa* would be more frequent. In a given safe site containing spores of *C. protrusa* and *C. tennesseensis*, it is likely that *C. tennesseensis* gametophytes would be mostly female while neighboring *C. protrusa* gametophytes would be primarily male. If this scenario is accurate, one would predict that *C. protrusa* should be the male parent in most crosses.

Extending this argument to the origin of *C. tennesseensis*, it may be predicted that *C. bulbifera* would be the egg parent in most cases. This hypothesis could be tested using information from chloroplast DNA (cpDNA) sequence variability.

TABLE 6. Population genetics statistics. Calculation of Nei's genetic identity and distance between infraspecific populations. Identity measures above the diagonal, distance measures below the diagonal.

Cystopteris bulbifera

Population number	1	2	3	4
1	—	0.7356	0.7716	0.8103
2	0.3071	—	0.9203	0.8734
3	0.2592	0.0830	—	0.8474
4	0.2104	0.1353	0.1656	—

Mean genetic identity = 0.8264

Cystopteris protrusa—RAMET POPULATIONS

Population number	1	2	3	4	5	6
1	—	0.9857	0.9161	0.8518	0.8940	0.7917
2	0.0144	—	0.9219	0.8313	0.9191	0.7937
3	0.0876	0.0813	—	0.8578	0.8475	0.7599
4	0.1604	0.1848	0.1534	—	0.7791	0.8271
5	0.1120	0.0844	0.1655	0.2496	—	0.7280
6	0.2336	0.2310	0.2745	0.1898	0.3174	—

Mean genetic identity = 0.8470

Cystopteris protrusa—GENET POPULATIONS

Population number	1	2	3	4	5	6
1	—	0.9280	0.9449	0.8253	0.8769	0.7670
2	0.0747	—	0.9275	0.7534	0.9364	0.7708
3	0.0567	0.0753	—	0.8840	0.8674	0.7765
4	0.1920	0.2832	0.1233	—	0.7285	0.7886
5	0.1313	0.0657	0.1423	0.3167	—	0.7371
6	0.2652	0.2603	0.2530	0.2375	0.3050	—

Mean genetic identity = 0.8342

Recent analyses (Stein & Barrington, 1990) indicated that cpDNA is inherited uniparentally in ferns (but see Andersson-Kottö, 1930). If cpDNA is carried in the egg, most *C. tennesseensis* plants should contain the chloroplast genome of *C. bulbifera*.

The available data indicate that *C. tennesseensis* is a relatively young species. The range of the derived allotetraploid *C. tennesseensis* extends only slightly beyond that of its diploid progenitors (Figs. 2–4). Further, *C. tennesseensis* shows no evidence of gene silencing. For the enzymes surveyed, all plants displayed fixed heterozygotic banding patterns that were additive for bands found in the diploid progenitors. All variability in the tetraploid could be attributed to recurring hybridization between genetically different diploid ancestors. All of these features are those anticipated for allopolyploids having recent origins (Haufler & Werth, 1986).

GENETICS

The mean levels of polymorphism and allelic variability for *C. protrusa* and *C. bulbifera* (Table 5) are similar to those expected of long-lived perennials (P = 0.66, A = 2.07) having a primarily outcrossed breeding system (P = 0.51, A = 1.85) (Hamrick et al., 1979). Based on calculations of mean observed and expected heterozygosity values (Table 5), neither diploid species appears to have an excess or deficiency of heterozygosity relative to Hardy-Weinberg expectations. The mean genetic identity among populations (Table 6: 0.8359) is at the lower end of that found among other fern species (I = 0.912, range = 0.78–0.99 in Soltis & Soltis, 1989). Table 7 lists the values of *F* and indicates which of these values represents a significant departure from zero. Those values that do not depart from zero are consistent with random mating for the species. Only the ramet populations

TABLE 7. Population genetics statistics. Calculation of the fixation index by population. Values not calculated for invariant loci. Asterisks after values = chi-square test. No asterisk indicates that the locus did not differ significantly from 0 and thus suggests random mating. * indicates significance at the $P < 0.05$ level; ** indicates $P < 0.01$ level; *** indicates $P < 0.001$ level.

Cystopteris bulbifera

Population number	PGI-2	IDH	SkDH	PGM-2	TPI-2	LAP
1	0.1806	0.0941	−0.0606	−0.2500	0.1923	0.4582
2	0.3836**	0.5220***	−0.0167	0.2458	0.3324*	0.0000
3	−0.3125	−0.3208	0.0000	−0.1053	0.0000	0.3000
4	−0.0952	−0.3450	−0.0952	−0.2778	0.0000	−0.0455

Cystopteris protrusa—RAMET POPULATIONS

Population number	PGI-2	IDH	SkDH	PGM-1	PGM-2	TPI-1	LAP
1	0.0437	−0.0781	0.0000	−0.1228	0.0000	0.5071***	0.6697***
2	0.0000	0.0000	0.0000	0.0000	0.0000	0.3478	1.0000***
3	−0.0606	0.0000	−0.6667**	−0.9444***	0.0000	−0.6667**	−0.6667**
4	−0.5972*	0.0336	0.0000	0.5175	−0.3529	0.0000	0.4202
5	0.5476	−0.0556	0.4328	0.0000	0.0000	0.7467*	−0.1343
6	0.0627	0.0000	0.0784	0.0000	0.0000	−0.2703	0.0000

Cystopteris protrusa—GENET POPULATIONS

Population number	PGI-2	IDH	SkDH	PGM-1	PGM-2	TPI-1	LAP
1	0.0114	0.0000	0.0000	0.1944	0.0000	0.6420*	0.7100**
2	0.0000	0.0000	0.0000	0.0000	0.0000	0.4444	1.0000
3	0.0000	0.0000	0.0000	−0.5000	0.0000	0.0000	0.0000
4	−0.2222	0.5926	0.0000	0.5926	−0.2222	0.0000	0.6857
5	0.3500	−0.0833	0.3953	0.0000	0.0000	0.7111	−0.1143
6	0.2400	0.0000	0.1204	0.0000	0.0000	−0.2667	0.0000

of *C. protrusa* show a large number of significant figures. Two facts suggest that these values should not be used as evidence that *C. protrusa* deviates from random mating. First, the significant values are both positive and negative with a mean of −0.0687, a value that is very close to zero. Second, deviations from zero can be caused by oversampling of cloned genotypes. Examining the *F* values for the genet populations shows that the number of significant figures drops to only two. Thus, the overall *F* values (Table 7) indicate that breeding systems for both diploid species conform to random mating models.

Genetic analyses of sporophytic populations can be correlated with antheridiogen data and measures of genetic load to draw conclusions about the breeding systems of diploid members of the *C. tennesseensis* complex. Antheridiogen response data indicate that *C. protrusa* should be outcrossing while *C. bulbifera* should be inbreeding. Genetic load data suggest that both diploids should be outcrossing. As discussed above, chi-square tests of fixation index values (Table 7), however, indicate that neither diploid species deviates significantly from random mating. Thus it may be that genetic load has a stronger control over fern mating systems than does possession of an antheridiogen system. By combining laboratory study of gametophytes and isozymic analyses of natural sporophytic populations we can obtain a clearer understanding of the factors controlling breeding systems among these *Cystopteris* species (Schneller et al., 1990).

Although the lack of allelic variability in *C. tennesseensis* precluded the application of isozyme data to analysis of breeding systems, genetic load data do provide clues to possible reproductive modes of this tetraploid. Other studies of diploid/polyploid complexes (Masuyama, 1979; Masuyama et al., 1987), have shown that although diploid progenitors may have high genetic loads, polyploids derived from them do not. Our studies of the *C. tennesseensis* complex provided another example of this phenomenon. Isolated gametophytes of both diploids were incapable of forming sporophytes, presumably because of post-zygotic lethal genes. However, 25% of isolated *C. tennesseensis* gametophytes did yield sporophytes. It has been hypothesized that homoeologous chromosome sets may provide buffers against expression of lethals and thereby allow polyploids to inbreed even if their progenitors cannot (Haufler, 1989).

Our data indicate that genetic identity between the diploids is zero. Given that the enzymes we surveyed are considered to be evolutionarily conservative (Gillespie & Kojima, 1968), the lack of similarity between *Cystopteris* congeners is quite remarkable. Angiosperm congeners have much higher mean genetic identity values (0.67 in Crawford, 1983) than those of most ferns that have been examined (0.33 in Soltis & Soltis, 1989). For *Bommeria*, Haufler (1985) suggested that the low genetic identity among congeners could indicate that the morphological characters uniting the species resulted through convergent evolution and, therefore, that this genus was not monophyletic. Few would dispute, however, the clear relatedness of *Cystopteris* species. Apparently, the lack of homology between diploid genomes observed in the cytogenetic study extends to the isozyme data as well. Thus, these data support alternative hypotheses that either (1) speciation in ferns may be accompanied by greater isozymic divergence than is typical for angiosperms (Haufler, 1987), or (2) that most congeneric fern species diverged prior to most angiosperm congeners (Soltis & Soltis, 1989).

The extraordinary genetic divergence of the diploids ensures a fixed heterozygote pattern for all enzymes in the derived allotetraploid. Yet, as introduced above, there is variability among individuals of *C. tennesseensis* (Figs. 10–12). These variants do not segregate among gametophytic progeny (Fig. 13), and are a direct reflection of the variability observed among diploid populations. In *Asplenium*, Werth et al. (1985b) used such information to propose recurring origins of the allopolyploids. It seems clear that *C. tennesseensis* originated more than once; but, in contrast to the situation in *Asplenium*, there does not seem to be any geographic pattern to these variants. The lack of evidence for gene silencing and the fact that no orphan alleles were detected also suggests recent origins.

SYSTEMATICS

The current investigation did not result in revision of the current systematic treatment of members of the *C. tennesseensis* complex. It was possible, however, to clarify the genetics of species boundaries and identify biological factors that have contributed to confusion in species circumscriptions. Perhaps the most significant factor blurring the boundaries between species is the formation of interspecific backcross hybrids. We collected and positively identified hybrids between *C. tennesseensis* and each of its diploid progenitors. These sterile triploids are morphologically intermediate between the sexual species and, if they are not removed from consideration, can bridge the morphological gaps between what are otherwise reasonably distinct taxonomic entities.

When not confounded by hybrids, a suite of qualitative features clearly discriminates *C. protrusa* from *C. bulbifera* (presence or absence of glandular trichomes and bulblets, clear differences in rhizome characteristics). In addition, we have demonstrated genetically regulated differences in quantitative leaf features (Table 3, Fig. 1) and significant differences in spore size between diploids and tetraploids (Table 1). Thus, although the characters are subtle, it is possible to identify each species through awareness of cryptic morphological characteristics and recognition of backcross hybrids. If pteridologists hope to resolve significant evolutionary units it will be necessary to consider suites of qualitative differences, which are sometimes cryptic.

Cryptic features are even more important in the identification of tetraploid *C. tennesseensis* than they are in the diploids. Especially significant are spore characteristics, both in terms of detecting spore abortion in backcross hybrids and calculating size measurements for positive identification of ploidy level (Table 1). Somewhat problematic is our observation that spores of autotriploid *C. protrusa* can appear normal and can be quite large (Haufler et al., 1985). It is therefore important to consider the mean and standard deviation in developing an accurate assessment of the spore size (and thus the ploidy) of individual specimens.

Given the large genetic distance between the diploid congeners in the *C. tennesseensis* complex,

it is probable that they have been phylogenetically isolated from each other for a long time and may represent systematic poles of the genus. The magnitude of the genetic distance between the two diploid species might also lead to the conclusion that hybrids between them should be rare and allopolyploid derivatives unsuccessful. Stebbins (1980) suggested that most successful polyploids are not strict autopolyploids or allopolyploids, but occupy a position somewhere between these extremes. Yet, our evidence indicates that even the highly differentiated *C. protrusa* and *C. bulbifera* have a history of recurring hybridizations and allopolyploid initiation. The derivative allotetraploid *C. tennesseensis* appears to be a successfully fledged and vigorous young species. It is quite widespread, is beginning to extend beyond the region of origin, and appears to be exploiting a niche that is not inhabited by either parent: neither diploid is found in the drier, more disturbed localities characteristic of *C. tennesseensis*.

Conclusions

Morphometric, chromosomal, and isozymic analyses of the *C. tennesseensis* complex support the taxonomic treatment originally proposed by Shaver (1954). The present studies document the genetic distinctness of the diploids *C. protrusa* and *C. bulbifera* and confirm the hybrid origin of the tetraploid *C. tennesseensis*. Considering the limited geographic range of the tetraploid, its sympatry with its parental diploids, and the lack of gene silencing, it appears that this allotetraploid is of relatively recent origin(s). Our studies have also pinpointed why these three species continue to be misidentified and misinterpreted taxonomically. First, the diploid species have a rather plastic morphology that, though genetically determined, is subtle and may be modified by environmental conditions. Second, there are autotriploid individuals of *C. protrusa* that expand the range of variability for that diploid (Haufler et al., 1985). Third, outcrossing breeding systems (driven by antheridiogen systems and/or high genetic loads) may contribute to frequent formation of backcross hybrids. These sterile triploid individuals span the morphological gaps between species, obscuring the boundaries that separate these genetically discrete taxa. Fourth, through recurring allopolyploid events, *C. tennesseensis* has incorporated much of the genetic variability of the diploids into its populations. As a result, positive identification of taxa in this complex depends on observations of cryptic spore and leaf features.

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THE AMERICAN PARADOX IN THE DISTRIBUTION OF FERN TAXA ABOVE THE RANK OF SPECIES[1]

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ABSTRACT

Whereas the numbers of fern species in the eastern Paleotropics and the Neotropics are comparable, the diversity at the subgeneric and especially the generic level is much higher in the eastern Paleotropics. This unexplained phenomenon is termed the "American Paradox" in the present paper.

In editing or preparing accounts of the various fern families for the treatment of pteridophytes in the series "The Families and Genera of Vascular Plants" (Kramer et al., in press), I gave special attention to the distribution of the genera and infrageneric taxa throughout the world, especially on the major continents. The areas where genera had their major concentrations were specially noted. A somewhat unexpected picture emerged.

The poverty of species as well as superspecific taxa in the African fern flora compared with that of Madagascar, tropical Asia-Australasia, and the Neotropics is well known; it has also been documented in many groups of flowering plants. For comments and citations of further literature, see Parris (1985) for ferns and Richards (1973) for flowering plants. Another striking phenomenon, largely unnoticed, is the relative poverty of fern taxa above the rank of species in the warmer parts of the New World. In this paper I provide documentation for this "American Paradox."

SPECIES RICHNESS

Comparing the species richness of the New World fern flora with that of tropical Asia-Australasia (leaving out Africa as much as possible for reasons stipulated above) is not easy, as few genera or families of ferns have been critically revised recently on a worldwide scale. The figures in Table 1, unless they are derived from recent monographs, should be regarded as rough approximations, mostly based on the data assembled for the "Families and Genera" referred to above. But they are probably correct regarding order of magnitude. (For the classification underlying this and other tables and lists of taxa in the present paper, see the Appendix.) These figures show that the New World does not emerge with a poorer fern flora as a whole.

In species richness the two areas are fairly balanced, the difference in the sum being undoubtedly fortuitous. When large genera such as *Asplenium* and *Dryopteris* are revised, the balance will probably be in favor of the eastern hemisphere.

GENERIC DIVERSITY

The picture is very different when instead of the number of species, the number of genera present in the western vs. the eastern hemisphere (excluding purely African taxa) is compared. (See Table 2.)

Note that in Lomariopsidaceae, Cyatheaceae, and Polypodiaceae, for example, where the eastern Old World and the New World have equal or at least comparable numbers of species, the number of (sub)genera is much higher in the eastern Old World. When families with fewer than four genera, where the figures are less meaningful, are left out of consideration, the difference is particularly striking: out of 13 families, 10 are considerably more diversified at superspecific levels in the Old World than in the New World; two families, Pteridaceae and Vittariaceae, are about equal; only one, Hymenophyllaceae, is more diversified in the New World. In Hymenophyllaceae the supraspecific classification is not yet completely worked out because Iwatsuki's (1984) system is based chiefly on the Asiatic representatives, so the picture may change to become even more favorable for the New World.

A comparison of Tables 1 and 2 leads to the

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conclusion that the fewer genera present in the New World contain relatively more species than the more numerous genera of the Old World. This suggests an imbalance between specific vs. generic representation.

This picture is again found when pantropical genera with very uneven distributions are compared. In Table 3 such genera are listed; they have five or fewer species in one hemisphere, the remainder in the other hemisphere.

In addition, two genera should be mentioned that, although being well represented in the Old World, have many more species in the New World, viz. *Elaphoglossum* and *Polypodium*.

Infrageneric Diversity

Infrageneric diversity is more difficult to assess because many subgenera and sections of ferns are treated as full genera by authors more inclined toward narrow generic circumscriptions. Here I refer to subdivisons of genera that are rarely, if ever, treated as distinct genera by contemporary authors. It proved difficult to develop reliable figures for a basis; few cosmopolitan or pantropical genera have recently been revised complete with natural infrageneric classifications. Conclusions from the following figures must be regarded as preliminary, as the number of cases is small.

Anemia (Schizaeaceae): see Mickel (1962, 1981) and Tryon & Tryon (1982). Three subgenera, one pantropical, one American with a single African species, one purely American. The genus was, however, more widespread in the Old World in the Tertiary (see, e.g., Huang, 1981, p. 24).

Bolbitis (Lomariopsidaceae): see Hennipman (1977). Ten series were proposed; three in both the Old and the New World, three only in Africa and its islands, three exclusively in the Old World (excluding strictly African taxa), one only in the New World.

Elaphoglossum (Lomariopsidaceae): see Mickel & Atehortúa (1980). Nine sections were recognized; four are strictly neotropical, not surprising in view of the enormous species diversity in the New World, but the five others are also represented in the Old World.

Dryopteris (Dryopteridaceae): see Fraser-Jenkins (1986). This comprises 16 infrageneric units (sections, or subgenera not further divided into sections); one is north-temperate, six are on both sides of the Atlantic, eight only in the eastern and one (almost) confined to the western hemisphere.

Lindsaea (Dennstaedtiaceae): see Kramer (1957, 1967, 1972), Kramer & Tindale (1976). Twenty sections were recognized; two are only in the southwestern Pacific, two in Madagascar; of the others, four are present in the Old and the New World, ten in Asia-Australasia only (or, in very few cases, extending to Africa); only two are confined to the Neotropics.

Hymenophyllum (Hymenophyllaceae): see Iwatsuki (1984). Fifteen sections or subgenera with single sections; four are subcosmopolitan or pantropical, two only in the southwestern Pacific; of the others, four are confined to the Old World, three to the New World; here the distribution is approximately balanced.

Osmunda (Osmundaceae): various sources for classification. There are three subgenera, one worldwide, one north-temperate, and one in eastern Asia.

Unfortunately, no sufficiently reliable data are available for the following large, pantropical to subcosmopolitan genera where information on the distribution of their subdivisions would be useful: *Adiantum*, *Asplenium*, *Blechnum*, *Cheilanthes*, *Ctenitis*, *Diplazium*, *Grammitis*, *Polypodium*, *Pteris*, and *Tectaria*. Paleogean preponderance for supraspecific diversity seems

Table 1. Approximate numbers of species in some widely distributed fern families and genera.

Family/genus	Tropical Asia-Australasia	Neotropics
Cyatheaceae	ca. 200	ca. 205
Polypodiaceae	ca. 350	ca. 250
Thelypteridaceae	ca. 440	ca. 240
Adiantum (Pteridaceae)	ca. 40	ca. 100
Bolbitis (Lomariopsidaceae)	12	14
Cyclopeltis (Dryopteridaceae)	ca. 5	1
Elaphoglossum (Lomariopsidaceae)	ca. 50	ca. 350
Lindsaea (Dennstaedtiaceae)	62	48
Lomariopsis (Lomariopsidaceae)	5	ca. 15
Lygodium (Schizaeaceae)	14	ca. 8
Nephrolepis (Nephrolepidaceae)	ca. 12	ca. 10
Odontosoria (including *Sphenomeris*) (Dennstaedtiaceae)	7	8
Oleandra (Oleandraceae)	ca. 25	ca. 8
Schizaea (Schizaeaceae)	7	8
Totals	ca. 1,229	ca. 1,265

TABLE 2. Distribution of the genera of the fern families (excluding probable relict families). Genera not present in the tropics of Asia-Australasia and the Neotropics appear in the overall sums of genera but not in the three columns at the right.

Family	Number of genera	In both hemispheres	Old World only	New World only
Blechnaceae	9	2	4	1
Cyatheaceae (genera or sections; see Appendix)	4	3	1	0
Dennstaedtiaceae	16	11	4	1
Dryopteridaceae sens. lat.	45	18	18	9
Gleicheniaceae	5	3	2	0
Grammitidaceae	4	1	3	0
Hymenophyllaceae	8	5	1	2
Hymenophyllopsidaceae	1	0	0	1
Lomariopsidaceae	6	4	2	0
Marattiaceae	6	1	4	1
Nephrolepidaceae	1	1	0	0
Oleandraceae	3	1	2	0
Ophioglossaceae	3	2	1	0
Polypodiaceae (see Appendix)	32	5	21	6
Pteridaceae sens. lat.	33	10	11	12
Thelypteridaceae (see Appendix)	29	9	17	3
Vittariaceae	6	2	2	2
Totals	211	78	93	38

likely for *Pteris* and *Tectaria*, neogean for *Adiantum* and *Polypodium*.

At infrageneric levels, the preponderance of Asia-Australasia also seems to be present, but more weakly. This was to be expected in view of what was found for the distribution of species over the two hemispheres.

DISCUSSION

Is the "American Paradox" perhaps an artifact of different approaches of systematists working with Old World as opposed to New World ferns? It is true that certain taxonomists concentrating on Asiatic ferns have a much narrower concept of taxa on all taxonomic levels than most others; a prominent example is Ching (e.g., 1978). But the classification worked out for the "Families and Genera" from which the above figures have largely been taken is the result of a critical reevaluation of all genera. Even if this classification is not acceptable to others, it may be said with some confidence that it does not contain a bias toward either "splitting" or "lumping" for the classification of the Old World or New World ferns.

Is there an explanation for the "American Paradox"? At the moment I prefer not to make an attempt. Assuredly, the New World tropics must have been habitable for ferns as long as the Paleotropics, and they harbor relict taxa like Loxomataceae, Gleicheniaceae, and Marattiaceae that go far back in geological history. Yet the assortment of ferns belonging to the so-called higher leptosporangiates gives the impression of relatively recent speciation in comparatively few taxa of higher rank; many of them are also present in the Old World and perhaps have originated from there. An explanation will eventually have to come from geology, paleogeography, and paleoclimatology data. In light of what we know about the breaking up

TABLE 3. Genera of wide distribution but very unevenly distributed over the world, with most species in one hemisphere, fewer than six in the other hemisphere.

Predominantly eastern hemisphere (9 taxa):

Deparia
Dicranopteris
Diplopterygium
Lomagramma
Microlepia (native in New World?)
Platycerium
Thelypteris sect. *Cyclosoriopsis* (*Christella* as genus)
Thelypteris sect. *Stegnogramma* (or *Stegnogramma* as genus)

Predominantly western hemisphere (4 taxa):

Hemionitis (the sole Old World species perhaps misplaced in the genus)
Microgramma
Pleopeltis
Trichomanes (sensu Iwatsuki, 1984)

of Gondwanaland, the paradox is even more perplexing. For the moment it may suffice to bring the phenomenon, duly documented, to the attention of the botanical community, without indulging in insufficiently founded speculation.

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Appendix. Notes on the classification.

As the treatment of pteridophytes for the "Families and Genera of Vascular Plants" referred to above has not appeared as this paper goes to press, certain points in the system that underlie the figures given above are briefly indicated.

Cyatheaceae: the sections upheld by Holttum in Holttum & Edwards (1983) have been counted as genera, as a compromise between the concepts of Holttum's and of R. M. Tryon's school of tree-fern students.

Dryopteridaceae: the family is broadly circumscribed, following Sledge (1973); it includes the athyrioid and the onocleoid ferns as well as *Woodsia*.

Oleandraceae: excluded from Davalliaceae (like *Nephrolepis*).

Polypodiaceae: certain species groups often treated as genera, but provisionally retained as subordinate groups of *Polypodium* in the "Families and Genera," are here counted as equivalent to genera.

Pteridaceae: these are broadly circumscribed and include *Adiantum* and all so-called gymnogrammoid ferns.

Thelypteridaceae: only five genera are retained in the "Families and Genera," but many subgenera are recognized; these are here counted as full genera in accordance with other authors' views.

RECURRING HYBRID FORMATION IN A POPULATION OF *POLYSTICHUM ×POTTERI*: EVIDENCE FROM CHLOROPLAST DNA COMPARISONS[1]

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ABSTRACT

The origins of a population of the hybrid fern *Polystichum ×potteri* (*P. acrostichoides* × *P. braunii*) were explored through an examination of restriction fragment length polymorphisms in chloroplast DNA. We demonstrate that the hybrid individuals in this population each had one of the two possible parental chloroplast genomes. This result documented recurrent hybridization in the population, whereas isozymes and morphological data did not. As expected, the hybrids combined the length polymorphisms in ribosomal DNA detected in each parent. We suggest that inferences from chloroplast DNA data about evolution in lineages rich in hybrid species can be biased by inheritance of two chloroplast genomes in three or more different descendants of a paleopolyploid species.

Plant organelle inheritance has been the focus of many investigations. The vast majority of published reports has examined reciprocal hybrids produced by crossing (Gillham, 1978) or somatic hybrids produced by protoplast fusion (Pelletier, 1986), but some studies have used natural hybrids (Palmer et al., 1983). Patterns of chloroplast inheritance were first traced by using white and green plastids as parental markers; later they were traced using specific chloroplast gene products (Gillham, 1978). More recently, chloroplast DNA fragment profiles produced by digestion with restriction endonucleases (e.g., Conde et al., 1979; Hachtel, 1980) have proven valuable as genetic markers of chloroplasts.

Surprisingly little has been reported about the inheritance of organelles in ferns. Kirk & Tilney-Bassett (1978) cited only one study: the chloroplasts of *Phyllitis scolopendrium* (L.) Newm. (as *Scolopendrium vulgare* Sm.) were found to be inherited biparentally. However, in mature plants of the rare fern hybrid *Osmunda ×ruggii* R. Tryon (Tryon, 1940; Wagner et al., 1978), the chloroplast genome of only one parent was found (Stein, 1985). Hence, the pattern of chloroplast DNA inheritance in ferns warrants further investigation.

Interspecific hybrid plants may be difficult to detect by their morphology (Doyle & Doyle, 1988), or the parentage of apparent hybrids may be uncertain (Doyle et al., 1985; Hilu, 1988; Yatskievych et al., 1988). Evidence from molecular biology has been helpful in resolving these difficulties. Electrofocusing of the small subunit of the enzyme ribulose-1,5-bisphosphate carboxylase, a nuclear DNA encoded polypeptide, has identified parents of tobacco hybrids, and examination of the large subunit (which is chloroplast DNA encoded) has determined maternal parentage (Wildman, 1983). Hybrids have also been documented by demonstrating summation of two allozymes, each fixed in one of the parent species (Werth et al., 1985a). The combination of diagnostic lengths of ribosomal DNA fragments from each parent in an intergeneric hybrid has been used as evidence for hybridity (Doyle et al., 1985). This approach was particularly helpful in the detection of *Claytonia* hybrids, where morphology is variable (Doyle & Doyle, 1988). In addition, restriction site mutations in

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chloroplast DNA have identified one parent of a hybrid in a number of studies (e.g., Palmer et al., 1983; Hilu, 1988; Yatskievych et al., 1988).

Allopolyploidy is a prevalent mode of hybrid speciation in plants. Klekowski & Baker (1966) documented the frequent occurrence of high chromosome numbers in the homosporous ferns. Recent estimates suggest that 95% of pteridophytes are polyploid and that the majority of these are allopolyploids (Grant, 1977). Although some of these reported polyploids act as genetic diploids as measured by isozyme analysis (Haufler & Soltis, 1986; Wolf et al., 1987), numerous allopolyploid taxa have been documented by a variety of approaches (Wagner & Wagner, 1980; Barrington et al., 1989). One of the best-studied fern genera in which allopolyploidy has played an important role in speciation of the group is the Appalachian *Asplenium* complex. Morphological analysis, chromosome number and pairing behavior (Wagner, 1954), flavonoid studies (Smith & Levin, 1963), and isozyme analysis (Werth et al., 1985a) have all been used to demonstrate the allopolyploid nature of members of this genus. In this complex, recurrent origins of allopolyploidy have been demonstrated by Werth et al. (1985b). Their isozyme analysis revealed several different fixed heterozygotes, strongly suggesting that the allopolyploids have formed several times.

We have examined chloroplast DNA (cpDNA) and ribosomal DNA (rDNA) of members of a population of *Polystichum* ×*potteri* Barrington, which is the triploid hybrid between *P. acrostichoides* (L.) Roth (a diploid, $n = 41$) and *P. braunii* (Spenner) Fée (an allotetraploid, $n = 82$) (Barrington, 1986). This fern population was studied to address several questions: 1) Are chloroplasts inherited uniparentally in *Polystichum* species? 2) Does a population of hybrids have cryptic variation with respect to its chloroplasts? If both chloroplast genomes can be demonstrated in the population but in different hybrid individuals, then recurrent hybrid formation would be demonstrated. 3) Are there restriction fragment polymorphisms in the ribosomal DNA of the parents, and are these different fragments both present in the hybrid offspring as would be expected from the combining of two different nuclei? 4) Do differing cytoplasms alter the morphology of hybrids with the same nuclear genome?

In this study we show that chloroplasts appear to be inherited uniparentally in *Polystichum* and that recurrent hybrid formation can be documented by the presence of two chloroplast genomes in different individuals of a hybrid population. The hybrids also show the expected additivity of restriction fragment length polymorphisms in their ribosomal DNA. No effect of cytoplasmic inheritance on morphology of the hybrids was detected.

Materials and Methods

Leaves of individuals of *Polystichum acrostichoides*, *P. braunii*, and four of their hybrids, *P.* ×*potteri*, were gathered from the talus below the limestone-rich outcrops of Barnard Gulf, Barnard, Windsor Co., Vermont, in July 1984. There, ca. 150 hybrid individuals are distributed over at least 0.4 km of east-facing slope from the foot to near the rim of the small steep-sided valley. The hybrid individuals included in this study, *Barrington 1091*, *1094*, *1097*, and *1098*, were widely separated (at least 2 m apart). They were all morphologically documented as hybrids in earlier work (Barrington, 1986). At the same time, *Barrington 1094* was documented cytologically as triploid. The irregular meiotic pairing he observed is typical of a hybrid between an allotetraploid and a nonancestral diploid. Collections of leaves from the two parents from the same site provided the material used to document the progenitor species in this study.

Chloroplasts and nuclei were isolated from the leaves as described by Palmer & Stein (1982) and Palmer (1986). Briefly, the fronds were disrupted in a large volume-to-tissue ratio (450 ml to 25–40 g of tissue) of an isolation buffer containing polyethylene glycol (PEG; M.W. 3,500) using first a blender and then a Polytron. Unbroken cells and other cellular debris were removed by filtration through a sandwich of two layers of cheesecloth and one layer of Miracloth. Nuclei and chloroplasts were collected by centrifugation in a GSA rotor at 2,500 RPM and washed with a buffer containing PEG. The re-collected organelles were suspended in a small volume of wash buffer and applied to sucrose gradients. The gradients were prepared by layering 30% on 50% sucrose. Both steps contained PEG 6000, and the gradients were allowed to diffuse overnight at 4°C before use. Centrifugation at 25,000 RPM for one hour using an SW 27 rotor separated the chloroplasts, which banded at the gradient-step interface, from the nuclei, which pelleted. Both organelles were recovered, lysed, and the DNAs were prepared in CsCl-ethidium bromide gradients. After removal of the CsCl and the ethidium bromide, the nuclear DNAs were extracted with tris-buffered phenol and ether and exhaustively dialyzed.

Chloroplast and nuclear DNAs were digested with restriction endonucleases according to the

manufacturer's instructions. For the rDNA analysis the following eight enzymes were used: *Apa* I, *Bam*H I, *Bgl* I, *Bst*E II, *Eco*R I, *Hinc* II, *Sac* I, and *Xho* I. *Hind* III and *Pst* I were used to digest the cpDNAs. Our methods for electrophoresis, blotting, and Southern hybridizations are described in Yatskievych et al. (1988), Palmer (1986), and Palmer & Stein (1982). The cloned ribosomal DNA used was pHA1 (Jorgensen et al., 1987), which contains an entire repeat unit from pea; it was kindly provided by R. Cuellar.

Results and Discussion

Chloroplast DNAs from *Polystichum acrostichoides*, *P. braunii*, and the four hybrids were digested with *Hind* III and the resultant fragments separated by gel electrophoresis (Fig. 1). It is clear that the chloroplast DNA fragments of the two parental species are very similar, yet the chloroplast DNA of *P. braunii* differs from that of *P. acrostichoides* in having a band of 11.5 kb, and *P. acrostichoides* has a band of about 9.4 kb, which is lacking in *P. braunii*. The 9.4 kb fragment was most likely produced by an additional *Hind* III site in the 11.5 kb fragment, but the presence of the other fragment (which is likely to be 2.1 kb) could not be verified in this gel. Nonetheless, the two large fragments provide a clear criterion to distinguish the parental genomes. The fragment profiles reveal that two of the hybrids inherited the *P. braunii* chloroplast genome, whereas the other two contained the *P. acrostichoides* chloroplast DNA. *Pst* I digests demonstrated the same pattern of inheritance of parental cpDNA genomes in the hybrids.

Since only one parental chloroplast genome is found in each of the hybrids examined, it would appear that uniparental inheritance is characteristic of these ferns as well in *O.* ×*ruggii*. (Stein, 1985). A similar result has been found in a tree fern hybrid, *Cnemidaria horrida* (L.) K. Presl × *Cyathea arborea* (L.) Smith (Stein & Conant, unpublished). Such studies, which examine chloroplast DNAs from mature plants, do not rule out the possibility of chloroplast inheritance from both parents with subsequent sorting of the chloroplast types. However, in *Phyllitis scolopendrium* the mode of plastid transmission is apparently biparental, yet both green and pale plastids were maintained (not sorted) in the mature sporophytes (Andersson-Kotto, 1931). Examination of very young hybrid individuals by Southern hybridization would address this question. Duckett & Bell (1971) reported that male gametes of archegoniate plants often do not transmit plastids to the egg. Thus, despite the one report of biparental transmission of chloroplasts in ferns (Gillham, 1978), uniparental, maternal inheritance of chloroplasts in ferns seems more likely to be a common pattern.

We also examined nuclear ribosomal DNA cut with eight restriction enzymes for evidence of the hybrid nature of these plants (Fig. 2). Seven of the eight endonucleases did not reveal informative restriction fragment length polymorphisms. However, the restriction enzyme *Apa* I cut the ribosomal DNA in the two parental types to yield several similar large fragments (ranging from 14.7 kb to 4.0 kb) and also two small fragments of slightly different mobility, 1.6 kb in *P. acrostichoides* and 1.4 kb in *P. braunii*. These small fragments are both present in the hybrids, as expected for nuclear DNA. A similar additivity of different lengths of ribosomal DNA fragments was demonstrated in an intergeneric hybrid between *Tolmiea menziesii* and *Tellima grandiflora* (Saxifragaceae) by Doyle et al. (1985). It is likely that these small fragments come from the intergenic spacer region, which has been shown to be the most variable (Appels & Dvorak, 1982), and length variation in this region may be related to loss or gain of a subrepeat. In addition to the ribosomal DNA fragment additivity, starch-gel electrophoresis revealed that all four hybrids summed isozyme bands fixed in each progenitor species at PGM-1 and SkDH (Barrington, unpublished) but did not show differences in fixed heterozygosity. Thus, while the isozymes and the ribosomal DNA data both verified that these ferns were hybrids, only the chloroplast DNA analysis demonstrated that they were undergoing recurrent formation.

The morphology of the hybrids was examined by one of us (DSB), while only the other (DBS) was aware of the genetic makeup of the cytoplasm. The 26 morphometric characters evaluated to determine if the cytoplasm accounted for a shift in morphology toward that of the parent contributing the cytoplasm included 21 leaf size and shape characters, stomate length and width, sorus position, receptacle shape, and true-indusium diameter. No clearcut relationship between morphology and the cytoplasmic compositions was detected in a discriminant function analysis of the hybrids and their parents.

The discovery of two chloroplast genomes in the population of hybrid *P.* ×*potteri* suggests that examination of a number of hybrid individuals might be routinely carried out as a means of documenting parentage and demonstrating recurrent hybrid formation. For example, Stein & Conant (unpub-

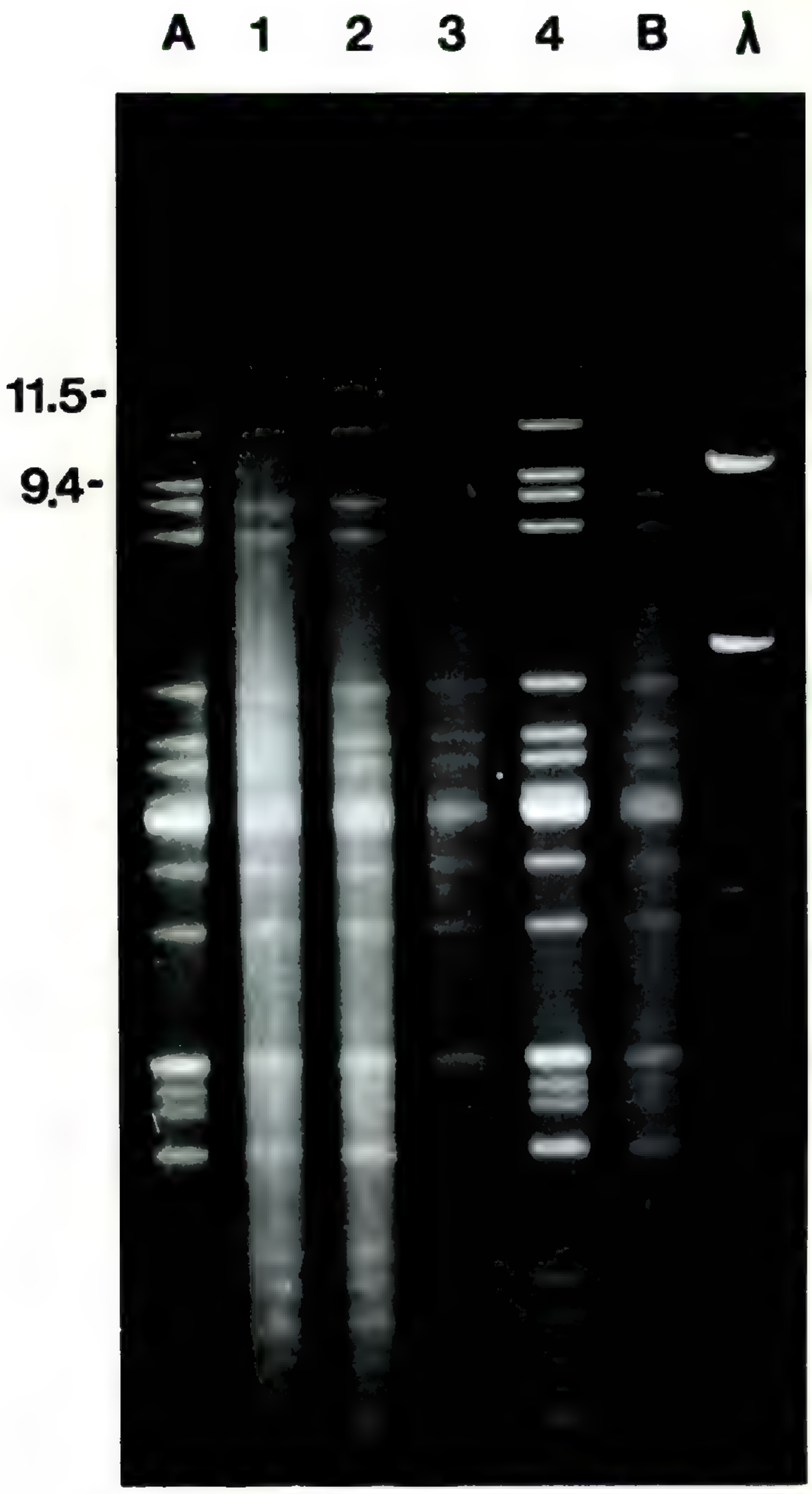

FIGURE 1. Chloroplast DNAs from *Polystichum acrostichoides* (A), *P. braunii* (B), and four hybrid plants of *P.* ×*potteri* (1, 2, 3, 4) digested with *Hind* III. The fragments were separated on 0.7% agarose by gel electrophoresis. Hybrids 1 and 2 contain the *P. braunii* chloroplast genome; hybrids 3 and 4 have the *P. acrostichoides* chloroplast genome. λ = λ DNA cut with *Hind* III. The bands in this lane correspond to (from the top) 23.1, 9.4, 6.6, 4.4, 2.3, and 2.0 kb.

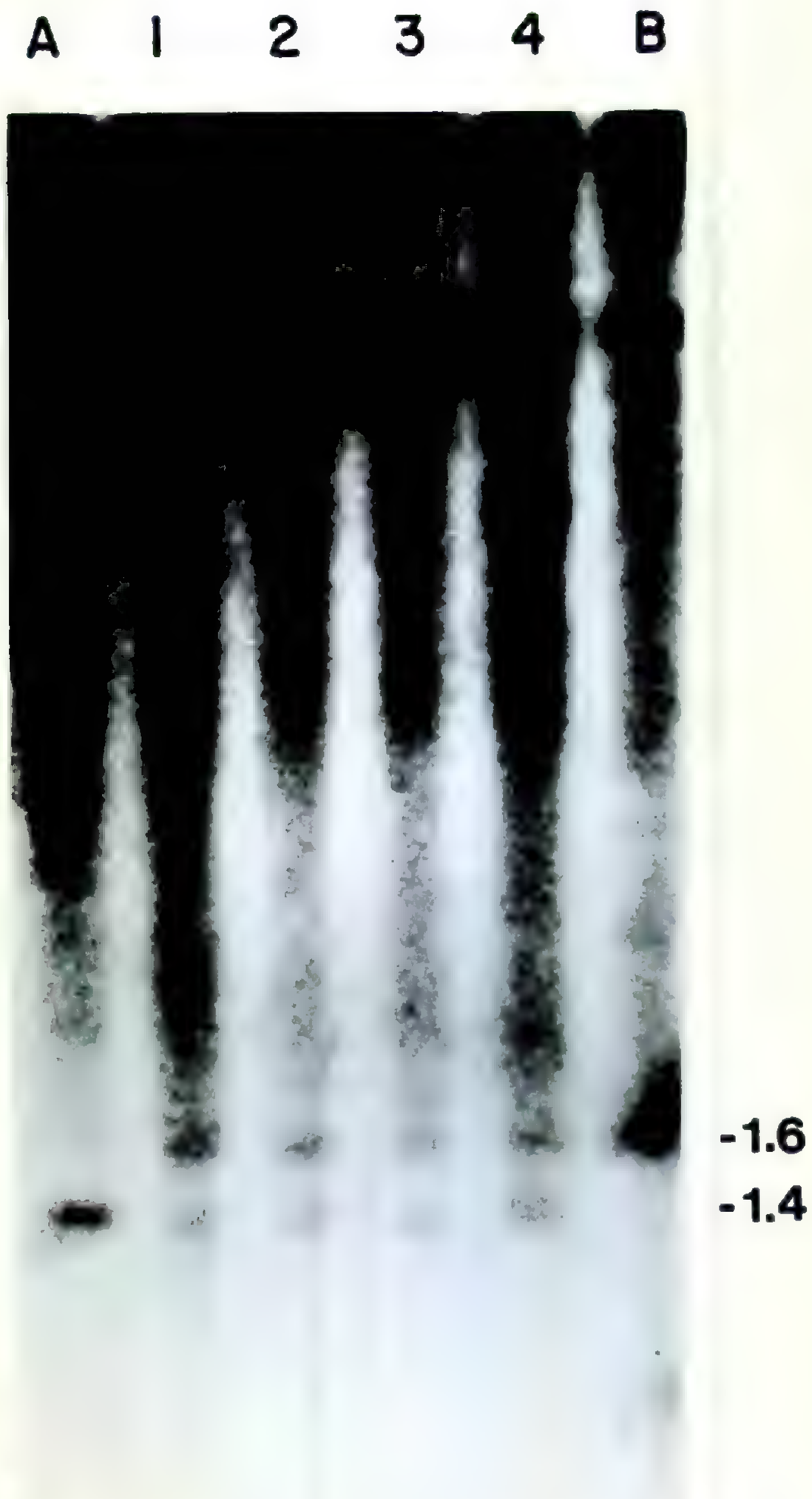

FIGURE 2. Ribosomal DNA fragment length polymorphisms in *P. acrostichoides* (A), *P. braunii* (B), and four hybrid plants of *P.* ×*potteri* (1, 2, 3, 4) digested with *Apa* I. The fragments were separated on 0.7% agarose, transferred to Zetabind by Southern blotting, and hybridized to a ^{32}P-labeled ribosomal DNA repeat (pHA1). *Polystichum acrostichoides* and *P. braunii* contain 1.6 kb and 1.4 kb fragments, respectively; the hybrids contain both fragment lengths.

lished), in a preliminary examination of the tree ferns, examined nine individuals of *Cnemidaria horrida* × *Cyathea arborea* for chloroplast DNA composition. Eight contained the chloroplast DNA of *Cnemidaria horrida*; the ninth revealed the chloroplast genome of *C. arborea*. This documents the second parent; but more importantly it shows that hybridization has occurred more than once in these tree fern hybrids.

Chloroplast DNA has also been examined in studies of polyploid species in other evolutionary groups. Bryophyte allopolyploids have been shown to have had multiple origins. In a study of *Plagiomnium medium* (Bruch, Schimper & Gumbel) Kop. (Wyatt et al., 1988), an analysis of isozymes and chloroplast DNA documented allopolyploidy and the maternal parent, respectively. Only one chloroplast DNA type was found, but the study does not state how many individuals were examined for their DNA composition.

Multiple origin of allopolyploids has recently been documented in several angiosperm taxa. R. Wallace & R. Jansen (in prep.) have used chloroplast DNA to demonstrate recurrent hybrid formation in *Microseris* (Asteraceae). An allotetraploid, *M.*

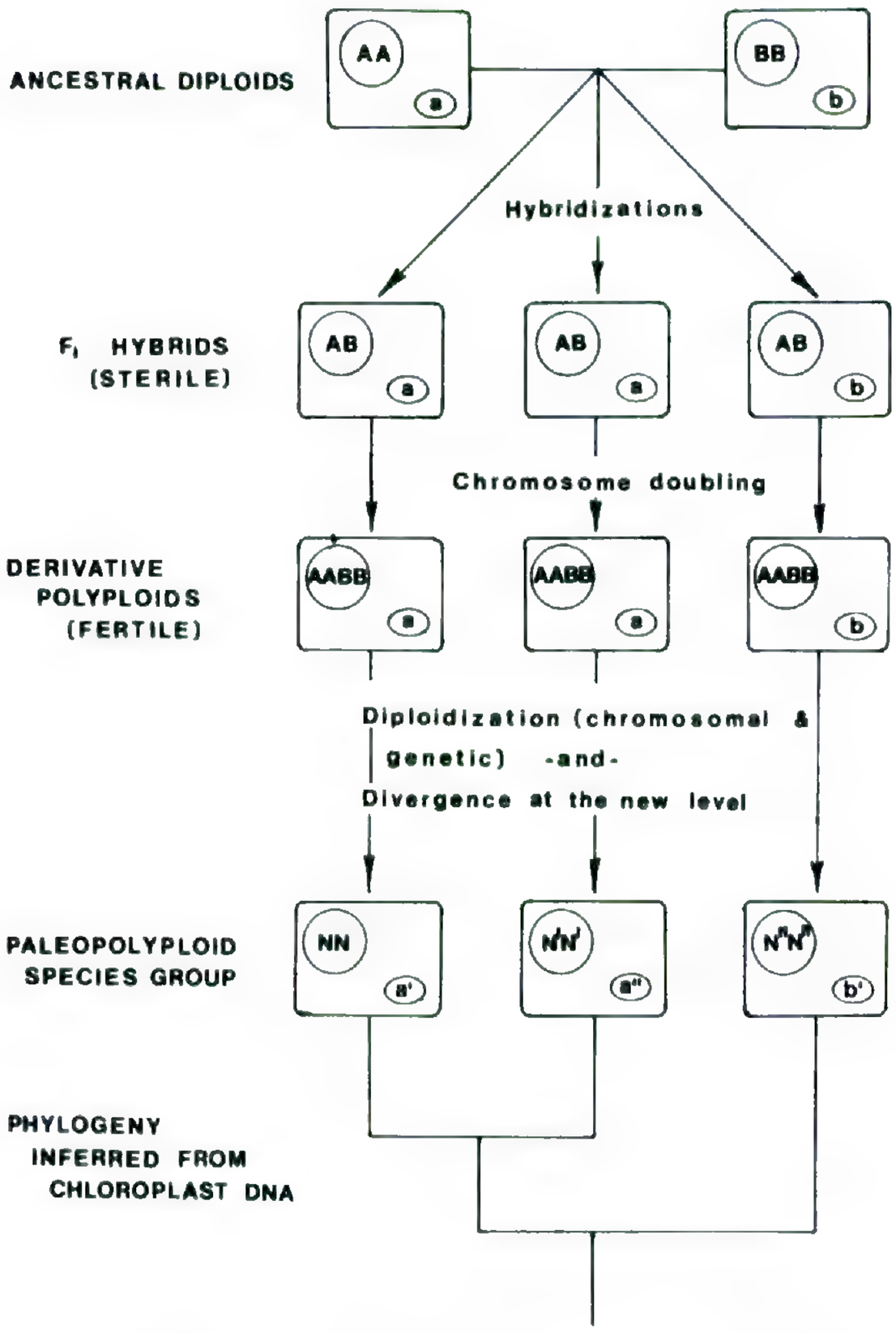

FIGURE 3. A hypothetical evolutionary history showing formation of paleoallopolyploids that subsequently gave rise to three modern species. In this case two of the modern species would contain chloroplasts derived from one chloroplast genome (e.g., the "a" chloroplast genome), whereas one of the modern species would have chloroplasts derived from a different chloroplast genome (e.g., the "b" chloroplast genome). Thus, relationships as measured by nuclear DNA would suggest equal divergence, whereas chloroplast DNA would support a closer relationship between two of the three descendants.

heterocarpa (Nutt.) K. Chambers, has originated twice. During each origin, the chloroplasts were contributed by different subspecies of *M. douglasii* (DC.) Schultz-Bip. (i.e., subsp. *douglasii* and subsp. *tenella* [Asa Gray] Chambers). No tetraploid so far examined has contained the chloroplast genome of *M. lindleyi* (DC.) A. Gray, the other progenitor of the tetraploid. Similarly, Doyle, Doyle, Brown, and Grace (pers. comm.) have provided evidence of multiple origin of allotetraploid *Glycine tabacina* (Labill.) Benth., taking advantage of cpDNA variation within one of the progenitors. In a cpDNA study of the *Tragopogon* polyploid complex, Soltis & Soltis (1989) found that the cpDNA genomes of the two progenitors (*T. dubium* Scop. and *T. pratensis* L.) are each represented in different populations of their allotetraploid *T. miscellus* Ownbey.

The fact that two chloroplast genomes exist in current populations of hybrids and allopolyploid species suggests that paleopolyploids (ancient polyploids whose progenitors are extinct) would have a high probability of having similar cryptic variation. Thus, measuring relationships with cpDNA comparisons could give differing patterns of relationship if two species were descended from tetraploids of similar ancestry but carrying different chloroplast genomes. Figure 3 illustrates a set of events that would yield such a spurious phylogeny. While such a scenario might be rare, it may be a useful model to consider when chromosome numbers suggest ancient polyploidy, as for example in the fern genus *Osmunda* (Wagner & Wagner, 1980).

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FELIX QUI POTUIT RERUM COGNOSCERE CAUSAS (VIRGIL).
(Photo taken by Walter H. Hodge.)

TURNERACEAE: NOVEDADES PARA LA GUAYANA VENEZOLANA[1]

María Mercedes Arbo[2]

Resumen

En Venezuela viven los dos géneros sudamericanos de Turneraceae: *Turnera* y *Piriqueta*. Las colecciones botánicas realizadas en los últimos años han proporcionado especímenes de siete nuevas especies de *Turnera*. Se propone una nueva combinación, *Piriqueta cistoides* subsp. *caroliniana* (Walter) Arbo. Se designa un neotipo para *P. undulata* Urban, porque el síntipo sobre el cual fue basado se destruyó en el herbario de Berlin.

Abstract

The botanical collections made in the Venezuelan Guayana during recent years have provided specimens representing seven new species of *Turnera*, described here: *T. annectens*, *T. argentea*, *T. castilloi*, *T. cicatricosa*, *T. huberi*, *T. paruana*, and *T. steyermarkii*. One new combination is proposed: *Piriqueta cistoides* subsp. *caroliniana* (Walter) Arbo. A neotype is designated for *Piriqueta undulata* Urban, because the syntype on which it was based was destroyed in the Berlin herbarium.

Turnera annectens Arbo, sp. nov. TIPO: Venezuela. Territorio Federal Amazonas: Cerro Sipapo (Paráque), frequent in savanna at 1,400 m, 1–3 Dec. 1948, *Maguire & Politi 27482* (holótipo, NY; isótipo, P). Figura 1.

Fruticulus 50 cm altus, ramis vetustioribus plicato-striatis, ramis hornotinis strigoso-pilosis. Folia lanceolata, elliptica vel obovata, glabra, nectariis destituta. Flores verisimiliter heterostyli; pedunculi liberi 10–30 mm longi; pedicelli nulli; prophylla cordata vel late ovata, acuta; calyx 25–27 mm longus; corolla lutea, petalis ad basin intus pilosis; filamenta basi tubo 1.5–2 mm tota facie adnata, et inter sese ± tubuli instar connata. Semina obovata, 3.2–3.5 mm longa, puberula, longitrorsum elevatim, transversim obsolete densissimeque striata.

Arbusto 50 cm de alto, ramas pardo-negruzcas, cilíndricas, marcada e irregularmente estriadas, algo lustrosas, glabras, entrenudos cortísimos, cicatrices foliares marcadas por estrías transversales profundas, lenticelas oblongo-lanceoladas marcadas por estrías transversales, ramas jóvenes rojizas con pubescencia estrigosa. Hojas con 1–2 yemas seriales, estípulas diminutas, cónicas o triangulares, 0.2–0.5 mm de largo, rojizas, pilosas; pecíolo 1.5–4 mm de largo, estrigoso; lámina lanceolada, elíptica u obovada, 30–62 mm de largo, 10–26 mm de ancho, coriácea, glabra o con algunos pelos simples en las venas, algo lustrosa, ligeramente maculada, base cuneada, margen subentero o serrulado, dientecillos glandulosos, ápice agudo, a veces obtuso, venas ligeramente salientes en la haz, prominentes en el envés, venas secundarias alternas o subopuestas, curvadas, ángulo de divergencia 40–50°, venas terciarias formando con frecuencia un ángulo de 90° con la vena media, venación menor conspicua en el envés. Alabastro recto, mucrones libres en el ápice. Flores solitarias, presumiblemente heterostilas (los especímenes estudiados presentaban flores brevistilas); pedúnculo 10–30 mm de largo, ligeramente estriado, estrigoso; pedicelo nulo; profilos 2, opuestos, dispuestos en la base del cáliz, ovados o cordiformes, 9–17 mm de largo, 7–12 mm de ancho, subglabros, base truncada, margen serrulado, ápice agudo o brevemente acuminado, sin apéndices basales; cáliz 25–27 mm de largo, tubo calicino 7.5–9 mm de largo, cilíndrico, con algunos pelos simples sobre las venas en la cara externa, glabro por dentro, lóbulos triangular-lanceolados, prefloración quincuncial, 3–5 nervados,

[1] Este trabajo fue realizado en gran parte en el Missouri Botanical Garden, con el apoyo de una beca de la fundación Jessie Smith Noyes. Agradezco a los curadores de los herbarios BM, BR, CTES, DS, F, FI, G, GOET, HBG, K, LIL, LY, M, MO, MY, NY, P, RB, S, US, VEN y W el préstamo del material estudiado; a la Dra. Alicia Lourteig su ayuda para identificar los tipos; y al Dr. William T. Stearn su guía para interpretar el material linneano. Las figuras 1 y 4 fueron preparadas por Víctor Maruñak y las figuras 2 y 3 por Bruno Manara.

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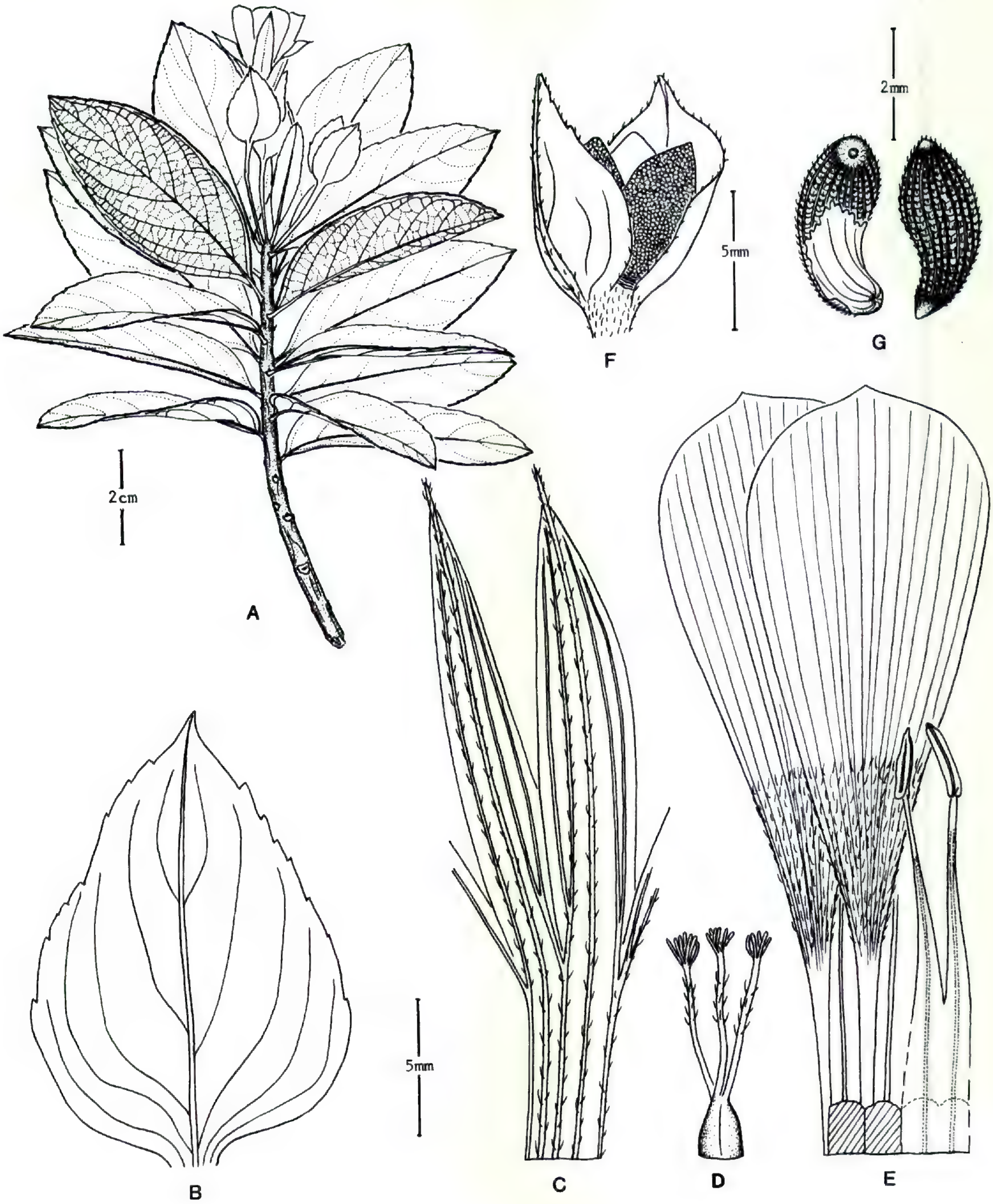

FIGURA 1. *Turnera annectens* (*Maguire & Politi 27482* P).—A. Rama florífera.—B. Profilo.—C. Porción del cáliz, cara externa.—D. Flor brevistila, gineceo.—E. Porción del tubo calicino, cara interna, con pétalos y estambres adnatos.—F. Cápsula con profilos.—G. Semillas con arilo.

mucronados (0.7–1.3 mm); corola amarilla, 2–3 mm más larga que el cáliz, pétalos con la uña soldada al tubo calicino, lámina obovada, base cuneada vellosa en la cara interna, ápice redondeado o brevemente acuminado; filamentos estaminales soldados en la base 1.5–2 mm al tubo calicino, complanado-subulados, glabros, 13–16 mm de largo en flores brevistilas, soldados entre sí por sus bordes a distintas alturas, ± hasta la mitad, formando un tubo desgarrado en 2–3 porciones; an-

teras triangular-subuladas, 2–2.8 mm de largo, 0.5 mm de ancho, base levemente emarginada, muy brevemente apiculadas, rectas; ovario ovoide o cónico, 2–2.5 mm de largo, 1.2–1.5 mm de ancho, glabro o con algunos pelos en el ápice, estilos 3, filiformes, pilosos en la porción media, 5 mm de largo en flores brevistilas, estigmas penicilados, 1 mm de largo. Cápsula elipsoide, 5 mm diám., valvas ovado-elípticas, cara externa pardo-rojiza, tuberculada, glabra, algo lustrosa. Semilla obovoide, 3.2–3.5 mm de largo, 1.4–1.7 mm de ancho, ligeramente curvada, castaña, con estrías longitudinales bien marcadas y estrías transversales muy tenues, pubérula, hilo amplio cónico, rafe linear poco marcada, cálaza saliente, deprimida en el centro; arilo membranáceo, unilateral, rasgado, llegando hasta la mitad de la semilla.

Material adicional estudiado. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro Sipapo (Paráque), occasional in Sabana Grande, vic. Campo Grande, 1,500 m, 21 Jan. 1949, *Maguire & Politi 28688* (P); Cerro Sipapo, East Basin Savannas, 1,900 m, 26–28 Jan. 1949, *Maguire & Politi 28672* (NY).

Esta especie, propia de la sabana, pertenece a la serie *Stenodictyae* Urban por tener el pedúnculo floral libre, carecer de pedicelo y presentar el episperma longitudinalmente estriado. Se distingue fácilmente por la ausencia de nectarios foliares y por sus profilos ovados de gran tamaño. Es la única especie del género que presenta los filamentos estaminales unidos entre sí a distintas alturas; este carácter la acerca a la serie *Annulares* Urban, cuyas especies tienen flores con los filamentos estaminales más o menos connados en la base. Su nombre, *annectens* (ligando, conectando), alude a la adhesión de los filamentos estaminales que la convierte en un nexo con la serie *Annulares*.

Turnera argentea Arbo, sp. nov. TIPO: Venezuela. Territorio Federal Amazonas: Dep. Atabapo, sabanas y bosques al E del Caño Perro de Agua, afluente derecho (oriental) del Río Orinoco, a unos 30 km al SE de la confluencia Orinoco–Ventuari, aprox. 03°47′N, 67°00′W, ca. 100 m, 30 Nov.–1 Dec. 1978, *Huber & Tillett 2809* (holótipo, VEN; isótipos, CTES, US). Figura 2A–E.

Frutex 1 m altus, pilis crispulis et aliis antrorsis densis obsitus. Folia linearia vel anguste elliptica, obtusa, longitudinaliter plicata, sericeo-velutina, margine integro. Flores verisimiliter heterostyli; pedunculi 1.5–2 mm longi, petiolo adnati; pedicelli nulli; calyx 7–7.7 mm longus, extus sericeo-velutinus; petala flava, intus ad medium usque pilosa; filamenta glabra subulata, basi tubo 0.5 mm tota facie adnata. Semina breviter obovata, 1.6–2 mm longa, vix curvata, brunnea, reticulata.

Arbusto 1 m de alto, tallo erecto, ramificado; corteza pardo-negruzca con estrías longitudinales marcadas y estrías transversales muy tenues, pelos crespos y otros largos antrorsos suberectos, muy densos, cicatrices foliares no prominentes. Estípulas subuladas, pilosas, 0.4 mm de largo. Yemas seriales 2, la basal florífera, la apical vegetativa. Pecíolo semicilíndrico; nectarios 2 en la unión de pecíolo y lámina, 0.3–0.4 mm diám., parte central cubierta con membrana rojiza, borde amarillento, pubérulo; lámina foliar verde-plateada, linear o angustielíptica, 10–27 mm de largo, 2–3 mm de ancho, longitudinalmente plegada, base atenuada, ápice obtuso, borde entero, haz y envés sericeo-velutinos, 6–7 pares de venas secundarias apenas visibles sobre el envés. Flores presumiblemente heterostilas (los ejemplares estudiados presentan flores longistilas), solitarias, amarillas, agrupadas en los extremos de las ramas; pedúnculo 1.5–2 mm de largo, soldado al pecíolo; profilos 2 en la base del receptáculo, subulados, 1.5–2.5 mm de largo, 0.3 mm de ancho, cara externa indumento como las hojas, cara interna glabra; pedicelo no desarrollado; cáliz 7–7.7 mm de largo, tubo calicino 3.5–3.7 mm de largo, cara externa sericeo-velutina, cara interna vellosa, lóbulos triangulares, bordes internos membranáceos, cara interna glabra, cara externa con indumento más largo que en el tubo; pétalos con la uña soldada al tubo calicino, lámina 4–5 mm de largo, 1–1.5 mm de ancho, obovada, cara superior con pelos largos en la base y sobre la vena media hasta la mitad; filamentos estaminales subulados, glabros, soldados en la base 0.5 mm al tubo calicino, 4–4.7 mm de largo en flores longistilas, anteras ovadas 0.7 mm de largo, dorsifijas, base emarginada, ápice apiculado; ovario 0.7–1 mm de largo, densamente piloso, placentas 3-ovuladas, estilos 3, cilíndricos, glabros, 3.5–4.2 mm de largo en flores longistilas, estigmas 1.2–1.5 mm de largo, penicilados, ca. 12 ramas. Cápsula 2.5–3 mm de largo, valvas lisas por fuera, con pelos simples crespos y otros largos antrorsos, cara interna lisa, lustrosa, amarillenta con manchitas oscuras irregulares. Semilla 1.6–2 mm de largo, 1.2 mm de ancho, ligeramente curvada, hilo cónico breve, cálaza saliente, oscura, cóncava, rafe linear, episperma pardo-negruzco reticulado, aréolas pequeñitas cuadrangulares o transrectangulares, muros longitudinales más notables que los transversales, arilo unilateral más corto que la semilla, membranáceo y blanquecino en seco.

Especie perteneciente a la serie *Leiocarpae* Urban por sus pedúnculos florales soldados a los pecíolos, pedicelos no desarrollados, frutos lisos y

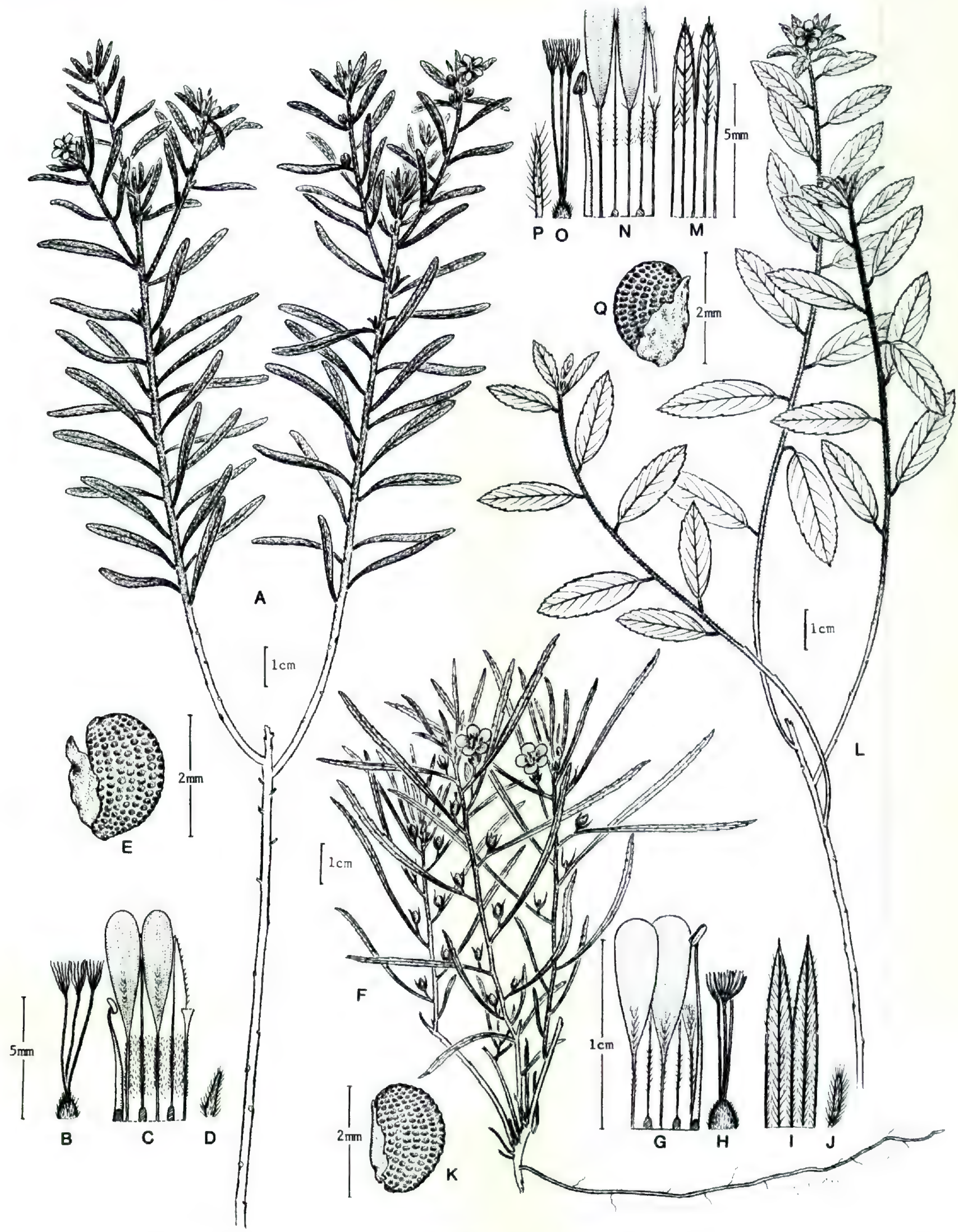

FIGURA 2. *Turnera argentea, T. huberi, T. paruana.* A–E. *T. argentea* (*Huber & Tillett 2809* VEN).—A. Hábito.—B. Flor longistila, gineceo.—C. Porción del cáliz, cara interna, con pétalos y estambre adnatos.—D. Profilo.—E. Semilla con arilo. F–K. *T. huberi* (F, *Huber 641* VEN; G–K, *Williams 12988* US).—F. Hábito.—G. Porción del tubo calicino, cara interna, con pétalos y estambre adnatos.—H. Flor brevistila, gineceo.—I. Porción del cáliz, cara externa.—J. Profilo.—K. Semilla con arilo. L–Q. *Turnera paruana* (*Huber 4386* VEN).—L. Hábito.—M. Porción del cáliz, cara externa.—N. Porción del tubo calicino, cara interna, con pétalos y estambre adnatos.—O. Flor longistila, gineceo.—P. Profilo.—Q. Semilla con arilo.

semillas reticuladas. Es afín a *T. elliptica* Urban de Goiás, Brasil, que se diferencia por sus hojas elípticas sésiles o subsésiles, 4–5 veces más anchas y aproximadamente de la misma longitud.

Turnera castilloi Arbo, sp. nov. TIPO: Venezuela. Territorio Federal Amazonas: Dep. Atures, Puerto Ayacucho, bosque húmedo del Río Cataniapo sector puente, margen izquierdo, 06°25′N, 67°25′W, 37 m, 14 Feb. 1983, *Castillo 1582* (holótipo, CTES). Figura 3A–F.

Frutex 1–3 m altus, pube simplici brevissima et aliis pilis curvato-erectis adspersus. Stipulae 0.6–0.9 mm longae. Folia elliptica vel ovata, subtus juxta marginem 14–20 nectariis orbicularibus minutis praedita; petiolus nectariis amplis marginibus glabris instructus. Flores heterostyli; pedunculi liberi 2–12 mm longi; pedicelli nulli; calyx 16–23 mm longus; petala aurantiaca, extus ad basin pilosa; styli pilis erectis hirsuti; filamenta glabra, basi tubo 0.6–1 mm facie externa adnata. Semina obovata, 2.7–3 mm longa, puberula, longitrorsum elevatim, transversim obsolete densissimeque striata.

Arbusto 1–3 m de alto, a veces ramas trepadoras, corteza castaña, tenuemente estriada, ramas cilíndricas, entrenudos de longitud variable, porciones con entrenudos cortos alternando con porciones con entrenudos largos, cicatrices foliares prominentes, ramas del año con indumento blanquecino, pelos cortísimos erectos y pelos cortos antrorsos. Estípulas triangular-subuladas, pilosas, 0.6–0.9 mm de largo. Yemas seriales 2, la basal florífera. Hojas coriáceas, lustrosas; pecíolo cilíndrico, 3.5–10 mm de largo, indumento como el tallo; 1–3 pares de nectarios sésiles, circulares o elípticos, opuestos o alternos, 0.7–2 mm de largo, con un reborde amarillento, glabro, lustroso, de ancho irregular, ubicados en la unión de pecíolo y lámina, los basales orientados lateralmente y los distales hacia el envés; lámina elíptica u ovada, 1.5–15 cm de largo, 0.6–4 cm de ancho, haz de color pardo-rojizo en seco, con máculas irregulares más claras, glabra o con algunos pelos simples sobre las venas, envés de color castaño, también con manchas irregulares más claras, algunos pelos simples sobre las venas, con nectarios sésiles, circulares, 0.4–0.5 mm diám., ubicados cerca del margen entre las venas secundarias y las escotaduras del borde; base cuneada o angostada, ápice acuminado o agudo, margen aserrado-crenado, venas prominentes en ambas caras, más en el envés, venas secundarias alternas u opuestas, ángulo de divergencia aprox. 75°, venas terciarias formando frecuentemente un ángulo de 90° con la vena media. Alabastros rectos con mucrones libres en el ápice. Flores solitarias, heterostilas, hojas tectrices a veces reducidas (15–20 mm de largo, 10–14 mm de ancho); pedúnculo cilíndrico, 2–12 mm de largo, indumento como el tallo; pedicelo nulo; profilos 2, opuestos, persistentes, situados en la base del cáliz, subulados, 2–3 mm de largo, 0.3–0.4 mm de ancho, pilosos, con 1–3 pares de apéndices basales laciniados; cáliz 16–23 mm de largo, tubo calicino cilíndrico, 6–10 mm de largo, cara externa con pelos cortos antrorsos, cara interna glabra, lóbulos triangulares o angustiovados, bordes internos membranáceos, ápice mucronado, mucrón 0.6–0.9 mm de largo, corola rojo-anaranjada, 1.5–2 mm más larga que el cáliz, pétalos con la uña soldada al tubo calicino, lámina obovada, 13–18 mm de largo, 3.5–5 mm de ancho, glabra por dentro, por fuera pilosa en la base; filamentos estaminales complanado-subulados, glabros, 5–5.5 mm de largo en flores longistilas, 12 mm de largo en flores brevistilas, soldados en la base 0.6–1 mm al tubo calicino, anteras 3–5.5 mm de largo, dorsifijas, filamento inserto a 1 mm de la base emarginada, ápice brevemente apiculado, recto después de la dehiscencia; ovario ovoide, 1.8–2 mm de largo, densamente estrigoso, estilos 3, cilíndricos, erectos, hirsutos en la porción basal y media, 6 mm de largo en flores brevistilas, 10–11 mm de largo en flores longistilas, estigmas 1–2 mm de largo, amarillos, penicilados. Cápsula 5 mm de largo, valvas ovadas, ápice agudo, cara externa parda tuberculada, con pelos simples cortos antrorsos, cara interna glabra, lustrosa, castaño-amarillenta. Semilla obovoide, 2.7–3 mm de largo, 1.6–1.8 mm de ancho, ligeramente curvada o recta, episperma con estrías longitudinales bien marcadas y estrías transversales tenues, con pelos cortísimos crespos, cálaza prominente, deprimida en el centro, rafe linear, hilo cónico breve; arilo membranáceo, envolvente, rasgado, más desarrollado sobre la rafe, casi tan largo como la semilla.

Material adicional estudiado. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dep. Atures, Puerto Ayacucho, bosque húmedo del Río Cataniapo entre la comunidad de las Pavas y la Reforma, 06°25′N, 67°25′W, 37 m, 18 Feb. 1983, *Castillo 1618* (CTES, MO); Puerto Ayacucho, Samariapo, a 100 km del puente sobre el Río Cataniapo, ribera derecha cerca Caño Carinagua, 06°25′N, 67°25′W, 25 July 1981, *Castillo 1338* (CTES); Puerto Ayacucho, bosque húmedo del Río Cataniapo, comunidad de Las Pavas, 06°25′N, 67°25′W, 37 m, 6 Aug. 1982, *Castillo 1525* (CTES); Puerto Ayacucho, bosque húmedo del Río Cataniapo, entre Raudal Buosaujaka y comunidad de Las Pavas, 06°25′N, 67°25′W, 90–100 m, 13 Aug. 1986, *Castillo 2194* (CTES, MO).

Turnera castilloi pertenece a la serie *Stenodyctiae* Urban; las especies más afines son *T. aurantiaca* Benth. que se diferencia por sus pedúnculos

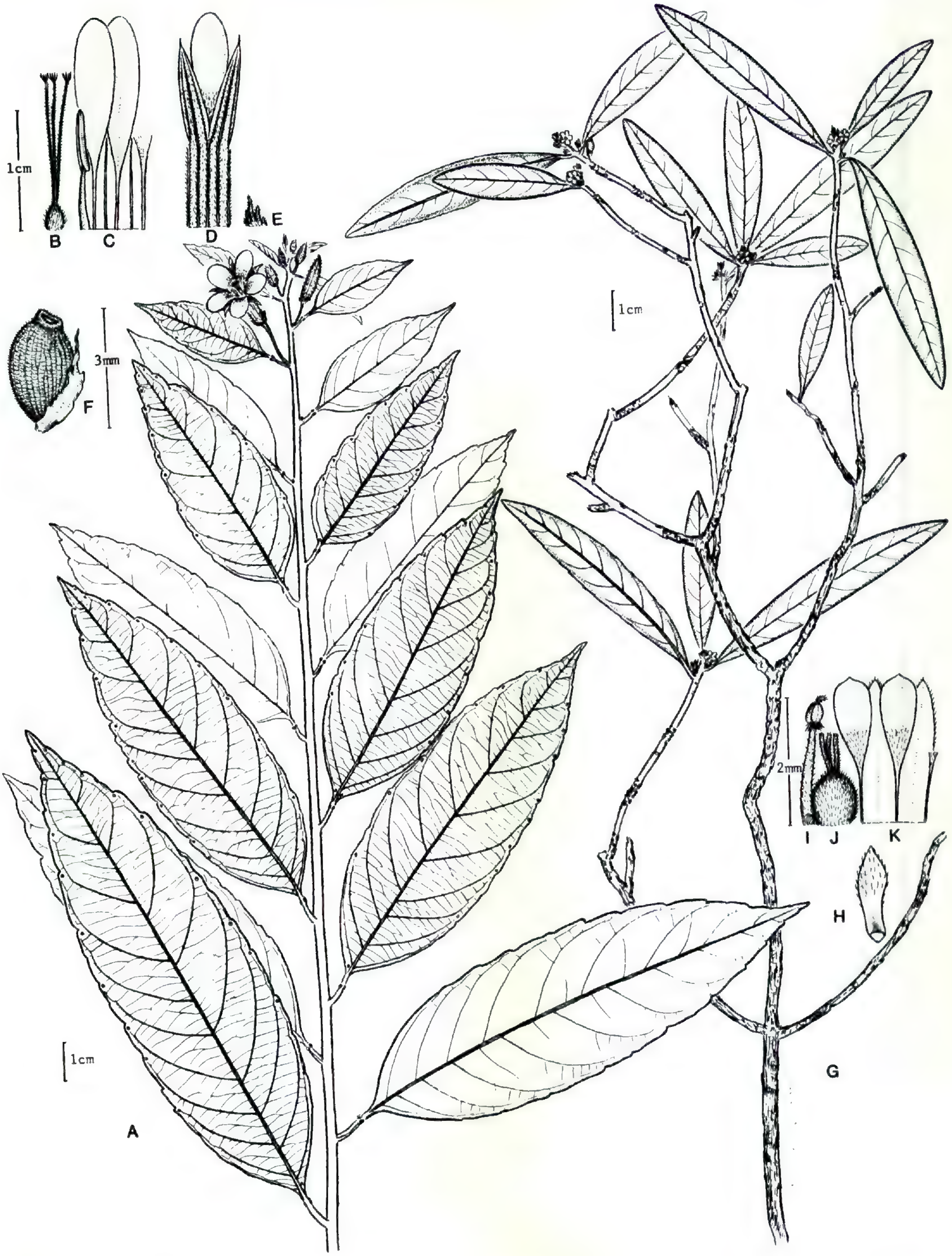

FIGURA 3. *Turnera castilloi*, *T. steyermarkii*. A–F. *T. castilloi* (A, *Castillo 2194*; B–F, *Castillo 1582* CTES).—A. Rama florifera.—B. Flor longistila, gineceo.—C. Porción del tubo calicino, cara interna, con estambre y pétalos adnatos.—D. Porción de cáliz y corola, cara externa.—E. Profilo.—F. Semilla con arilo. G–K. *T. steyermarkii* (*Bunting et al. 3671* MY).—G. Rama florífera.—H. Profilo.—I. Flor brevistila, estambre.—J. Flor brevistila, gineceo.—K. Porción del cáliz, cara interna, con pétalos adnatos.

florales 9–37 mm de largo y sus estilos generalmente glabros; *T. acuta* Willd. ex Schultes con profilos lanceolados u ovado-lanceolados 2–9 mm de ancho y estípulas 0.3–0.6 mm de largo y *T. macrophylla* Urban que posee nectarios de reborde piloso y cáliz corto 7–10 mm de largo. Dedico esta especie al Prof. Aníbal Castillo quien colectó los ejemplares estudiados.

Turnera cicatricosa Arbo, sp. nov. TIPO: Venezuela. Territorio Federal Amazonas: Río Orinoco, 1–10 km below San Fernando de Atabapo, 150 m, 11 May 1954, *Level 64* (holótipo, P; isótipo, NY). Figura 4.

Frutex 0.5–3 m altus, pilis crispulis brevissimis et aliis curvato-erectis intermixtis. Stipulae 1.5–3 mm longae. Folia subtus supra basin ad marginem nectariis discoideis glabris praedita. Flores heterostyli; pedunculi liberi 1–5 mm longi; pedicelli nulli; calyx 8–14 mm longus; corolla flavida; filamenta puberula; styli pilis erectis hirsuti. Semina obovata, 2.7–3.2 mm longa, glabra, longitrorsum elevatim, transversim obsolete densissimeque striata.

Arbusto apoyante, 0.5–3 m de alto, ramas cilíndricas, pardo-negruzcas o pardo-rojizas, marcada e irregularmente estriadas, lustrosas, glabrescentes, lenticelas suborbiculares u oblongo-lanceoladas, entrenudos de longitud variable, 1–35 mm de largo, cicatrices foliares salientes, ramas jóvenes levemente estriadas, rojizas, pubescentes a tomentosas, pelos cortos, crespos, entremezclados con otros más largos, simples, antrorsos. Hojas con 2 yemas seriales, la basal florífera, la apical a veces desarrollada en ramita florífera; estípulas persistentes, triangular-subuladas, rojizas o negruzcas, pilosas, 1.5–3 mm de largo; pecíolo canaliculado, pubescente a tomentoso, 1–7 mm de largo; lámina elíptica u oblongo-lanceolada, a veces obovada, 10–85 mm de largo, 6–30 mm de ancho, cartácea, haz pardo-rojiza, a veces maculada, levemente estriada en seco, con pelos simples curvado-antrorsos, envés pubescente, más densamente en las venas, a veces glabro, base atenuada o brevemente atenuada, a veces ligeramente auriculada, generalmente con un par de nectarios amarillentos, con borde glabro, situados sobre el envés, discoideos en hojas nuevas, margen simple o doblemente aserrado-crenado, ápice agudo, obtuso o brevemente acuminado, venas ligeramente hundidas en la haz, prominentes en el envés, venas secundarias alternas a subopuestas, ángulo de divergencia 35–50°, venas terciarias curvadas, con frecuencia dispuestas en ángulo recto con la vena media. Alabastros rectos, mucrones libres en el ápice. Flores solitarias, heterostilas; pedúnculo cilíndrico, 1–5 mm de largo, rojizo; pedicelo nulo; profilos 2, opuestos, dispuestos en la base del cáliz, lanceolados, 7–10 mm de largo, 1.5–3 mm de ancho, pilosos, margen dentado, dientes glandulosos, ápice agudo o acuminado, provistos de apéndices basales divididos en 2–3 lacinias subuladas, formando en conjunto un pseudocalículo persistente; cáliz 8–14 mm de largo, tubo calicino 4–7 mm de largo, piloso por fuera excepto en la base, velloso por dentro en la porción apical, lóbulos angusti-triangulares, preflo-ración quincuncial, trinervados, pilosos en la cara externa y glabros en la interna, mucrón 0.5–0.7 mm de largo; corola amarilla, a veces blanquecina, 3–4 mm más larga que el cáliz, pétalos con la uña soldada al tubo calicino, lámina obovada, 7–12 mm de largo, 3–4.5 mm de ancho, haz pilosa en la base, ápice redondeado o brevemente apiculado; filamentos estaminales soldados en la base 1–1.5 mm al tubo calicino, complanado-subulados, 7–11 mm de largo en flores brevistilas, 6–7 mm de largo en flores longistilas, pubérulos, anteras dorsifijas, elíptico-lanceoladas, 3–4 mm de largo, 0.7 mm de ancho, base emarginada, brevemente apiculadas, rectas o curvadas después de la dehiscencia; ovario ovoide, 1.5–1.8 mm de largo, 1–1.3 mm de ancho, densamente estrigoso, ca. 20-ovulado, estilos 3, filiformes, hirsutos, 12 mm de largo en flores longistilas, 3–5 mm de largo en flores brevistilas, estigmas penicilados 1–1.5 mm de largo. Cápsula ovoide o globosa, 3.5–5.5 mm de largo, 3–4.5 mm de ancho, valvas ovadas, cara externa pardo-amarillenta, tuberculada, pilosa, cara interna glabra, lustrosa, amarillenta. Semilla obovoide, 2.7–3.2 mm de largo, 1.2–2 mm de ancho, curvada, castaña, con estrías longitudinales bien marcadas y estrías transversales muy tenues, glabra, hilo cónico, rafe linear apenas marcada, cálaza saliente deprimida en el centro, arilo membranáceo, unilateral, rasgado, tanto o más largo que la semilla.

Material adicional estudiado. VENEZUELA. BOLÍVAR: Río Caroní, cerca de la boca de Tirika (Guayana), 400 m, May 1945, *Cardona 1169* (US); en playas de la Isla Maripa, Alto Caroní, 370 m, 18 Feb. 1953, *Cardona 2830* (MO); Distr. Piar, Cerro Kurún-tepui, aprox. 17 km E de Canaima, 06°14′N, 62°43′W, 1,050 m, 31 Aug. 1983, *Huber et al. 8191* (CTES); Distr. Piar, vicinity of Guadequen (Buadequen), Río Acanán, affluent of Río Carrao, W of Cerro Los Hermanos, 05°56′N, 62°17′W, 1–3 May 1986, *Steyermark et al. 131899* (MO). GUYANA. ESSEQUIBO: Pakaraima Mountains, Imbaimadai savannas, upper Mazaruni River, 550 m, 21 Oct. 1951, *Maguire 32173* (NY, P).

Esta especie ha sido coleccionada en Venezuela y Guyana, en selvas marginales y sabanas. Es muy afín a *T. acuta* Willd. ex Schultes, que se diferencia por los profilos anchos y las estípulas cortas 0.3–0.6 mm de largo, y a *T. macrophylla* Urban que

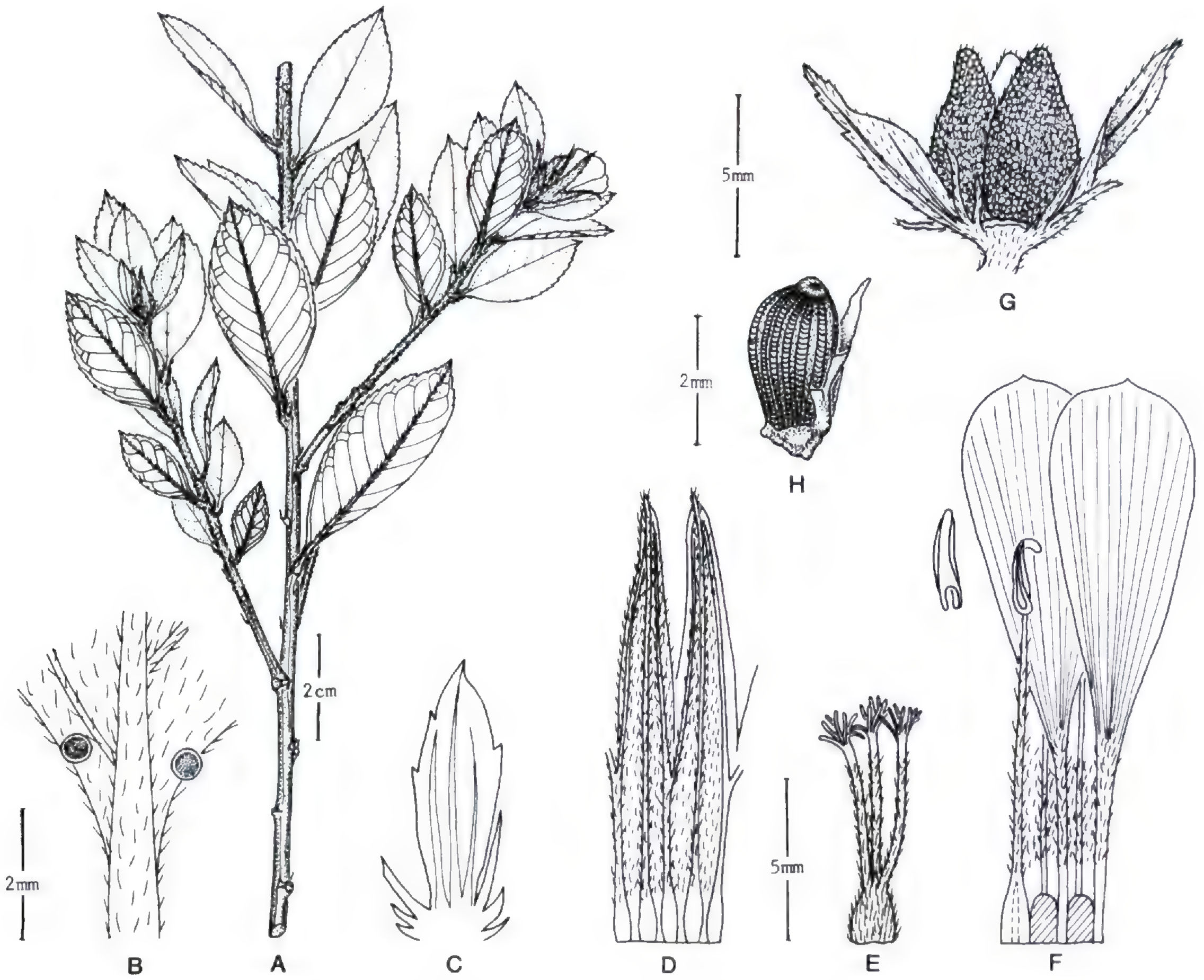

FIGURA 4. *Turnera cicatricosa*.—(A, *Maguire 32173* P; B–H, *Level 64* P).—A. Rama florífera.—B. Detalle del envés foliar mostrando los nectarios.—C. Profilo.—D. Porción del cáliz, cara externa.—E. Flor brevistila, gineceo.—F. Porción del tubo calicino, cara interna, con estambre y pétalos adnatos.—G. Cápsula con profilos.—H. Semilla con arilo.

se distingue por sus nectarios foliares con borde piloso y sus frutos grandes. *T. castilloi*, también afín, presenta 14–20 nectarios diminutos en el envés, cerca del margen foliar.

Turnera huberi Arbo, sp. nov. TIPO: Venezuela. Territorio Federal Amazonas: Estación de Piscicultura de Puerto Ayacucho, entre la carretera hacia Samariapo y la pista de aterrizaje de Puerto Ayacucho, aprox. 05°37′N, 67°36′W, aprox. 75 m, 16 Apr. 1977, *Huber 641* (holótipo, VEN). Figura 2F–K.

Herba vel fruticulus 13–40 cm altus, pilis crispulis brevibus et aliis curvato-erectis indutus. Folia linearia vel anguste elliptica, 8–23-plo longiora quam latiora, acuta, margine plano denticulato. Flores heterostyli; pedunculi 3–6 mm longi, 0.5–4 mm petiolo adnati; pedicelli nulli; calyx 7–10 mm longus, extus densissimeque pilosus; corolla flava; filamenta glabra, subulata, basi tubo 0.5–0.6 mm tota facie adnata; styli glabri. Semina breviter obovata, 1.8–2.2 mm longa, vix curvata, brunnea, reticulata.

Hierba o sufrútice 13–40 cm de alto, base leñosa, con xilopodio, tallos 1 a varios, 0.8–1 mm diám., ramas viejas con corteza rojiza, longitudinalmente estriada, ramas nuevas cilíndricas, con pelos simples crespos y otros más largos, antrorsos, muy densos hacia los ápices. Hojas con 2–3 pares de estípulas 0.1–0.3 mm de largo, cónicas, rojizas; yemas seriales 2, la basal florífera; pecíolo 1.5–3 mm de largo, semicilíndrico, indumento como el tallo; nectarios 2 en la unión de pecíolo y lámina o en la base de la lámina foliar sobre el envés, circulares o elípticos, 0.5–0.7 mm de largo, la parte central con una membrana provista de un poro, el borde pubérulo o en parte glabro; lámina foliar linear o angustielíptica, base cuneada o atenuada, 17–57 mm de largo, 2–5 mm de ancho, relación largo : ancho = 8–23 : 1, ápice agudo,

borde serrulado excepto en la base, haz punteada con algunos pelos simples especialmente sobre las venas y cerca del borde, vena principal prominente, 6–7 pares de venas laterales a veces ligeramente salientes, ángulo de divergencia muy agudo, envés con venas más prominentes, pelos simples y otros glandulares capitados sésiles; venación menor inconspicua. Flores solitarias, heterostilas; pedúnculo floral 3–6 mm de largo, soldado al pecíolo, la porción apical libre; profilos 2, subulados, 2–6 mm de largo, 0.4–0.6 mm de ancho, borde entero o serrulado, pilosos en ambas caras; pedicelo no desarrollado; cáliz 7–10 mm de largo, tubo calicino 3.5–5 mm de largo, cara interna con pelos blandos, cortos, por fuera con pelos cortos crespos, lóbulos triangulares o angustiovados, mucrón 0.5 mm de largo, cara interna glabra, cara externa con pelos simples crespos y pelos muy largos sobre las venas, bordes internos membranáceos; pétalos con la uña soldada al tubo calicino, lámina obovada angosta, 5–7 mm de largo, 1.5–2.3 mm de ancho, glabra o con algunos pelos en la base y sobre la vena media; filamentos estaminales soldados en la base 0.5–0.6 mm al tubo calicino, 5–9.7 mm de largo en flores brevistilas, 4.5 mm de largo en flores longistilas, anteras angustiovadas o elípticas, 0.7–1.2 mm de largo, dorsifijas; ovario cónico 1–1.5 mm de largo, densamente piloso, placentas 3–4 ovuladas, estilos 3, cilíndricos, glabros, 3–5 mm de largo en flores brevistilas, 5 mm de largo en flores longistilas, estigmas 1.7–2 mm de largo, penicilados, ca. 12 ramas. Cápsulas 2–4 mm diám., valvas ovadas, por fuera lisas, pilosas, castañas o amarillentas, por dentro lustrosas, jaspeadas. Semillas obovoides, 1.8–2.2 mm de largo, 1–1.2 mm de ancho, ligeramente curvadas, hilo cónico breve, cálaza pigmentada, ligeramente saliente, generalmente cóncava, rafe linear, episperma reticulado, pardo, aréolas cuadrangulares o rectangulares; arilo unilateral casi tan largo como la semilla o ligeramente mayor, blanquecino en seco.

Material adicional estudiado. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Estación de Piscicultura de Puerto Ayacucho, entre la carretera hacia Samariapo y la pista de aterrizaje de Puerto Ayacucho, aprox. 05°37′N, 67°36′W, aprox. 75 m, 19 Apr. 1977, *Huber 693* (VEN); alrededores de Campo Florido, en carretera hacia El Sipapo, ca. 6 km después del cruce desde la carretera Puerto Ayacucho–Samariapo, 22 Mar. 1979, *Trujillo & Pulido 15152* (MY); Puerto Ayacucho, 100 m, 18 May 1940, *Williams 12988* (US), *12989* (VEN).

En esta especie, perteneciente a la serie *Leiocarpae* Urban, la heterostilia está poco diferenciada, pues especialmente en los ejemplares brevistilos, anteras y estigmas están parcialmente en contacto. La diferencia en longitud hallada entre androceo y gineceo es de 1–2 mm en flores longistilas y de 0.7–2 mm en flores brevistilas. Especie afín a *T. lanceolata* Cambess. del centro de Brasil, que se diferencia por su tallo aristado y por sus hojas con pecíolos cortos y venación conspicua en ambas caras. También está emparentada con *T. argentea*, que se diferencia por sus hojas seríceas, obtusas, y de borde entero. Dedico esta especie al Dr. Otto Huber quien coleccionó el ejemplar tipo y numerosos especímenes de Turneráceas.

Turnera paruana Arbo, sp. nov. TIPO: Venezuela. Territorio Federal Amazonas: Dep. Atabapo, Serranía del Parú (Aroko), sabanas sobre colinas onduladas en el sector centro-nororiental de la serranía, al S del Río Parú, aprox. 04°33′N, 65°31′W, 710 m, 5–6 Oct. 1979, *Huber 4386* (holótipo, VEN). Figura 2L–Q.

Frutex 50 cm altus, pilis crispulis brevibus et aliis curvato-erectis praeditus. Folia elliptica, supra subglabra, subtus supra basin ad marginem nectariis glabris praedita. Flores verisimiliter heterostyli; pedunculi 1.2–2.5 mm longi adnati; pedicelli nulli; calyx 7.5 mm longus, extus ad basin glaber; corolla flava; filamenta glabra, subulata, basi tubo 0.3 mm tota facie adnata; semina breviter obovata, 1.8 mm longa, vix curvata, brunnea, reticulata.

Arbusto 50 cm de alto, ramificado, tallo cilíndrico, parte basal con corteza rojiza con grietas longitudinales, cicatrices foliares no salientes, pelos crespos cortos y pelos largos antrorsos o erectos. Hojas obscuras en seco, en vivo haz verde mediano, envés verde claro; estípulas 0.5 mm de largo, subuladas; yemas seriales 2, la basal florífera, la apical vegetativa; pecíolo semicilíndrico 2–4 mm de largo; lámina elíptica 15–30 mm de largo, 6–11 mm de ancho, relación largo : ancho = 2.5–3 : 1, base brevemente atenuada, ápice agudo, borde piloso plano, serrulado, dientes agudos terminados en una emergencia subulada, haz lustrosa, pardo-rojiza, glabra excepto algunos pelos sobre la vena media y cerca del borde, 6–9 pares de venas laterales apenas salientes, envés castaño, vena principal y secundarias prominentes, con pelos largos, simples, antrorsos, ángulo de divergencia 45–50°, venas terciarias visibles, no prominentes, venación menor inconspicua; nectarios 2, situados en la base de la lámina, sobre el envés, elípticos, 0.6–0.9 mm de largo, parte central cubierta con una membrana blanquecina, borde rojizo glabro. Flores presumiblemente heterostilas (el ejemplar estudiado presenta flores longistilas), agrupadas en racimos apicales hojosos, flores basales alejadas; hojas floríferas apicales bracteiformes, obovadas u romboidales, 7–

12 mm de largo, 3–5 mm de ancho; pedúnculo floral totalmente soldado al pecíolo, 1.2–2.5 mm de largo; profilos 2.5–3.5 mm de largo, 0.3–0.4 mm de ancho, subulados, rojizos, uninervados, con pelos largos y simples en los bordes y en la cara externa, insertos en la base del receptáculo; pedicelo ausente; cáliz 7.5 mm de largo, tubo calicino 4.3 mm de largo, glabro por fuera en la base, con algunos pelos cortos sobre las venas en la parte superior, por dentro velloso en la porción media, lóbulos triangulares, glabros por dentro, por fuera con pelos simples largos especialmente sobre las venas; corola amarilla, pétalos con la uña soldada al tubo calicino, lámina con algunos pelos en la base, en la cara interna; filamentos estaminales subulados, glabros, soldados en la base 0.3 mm al tubo calicino, 5 mm de largo en flores longistilas; anteras ovadas, 1 mm de largo, 0.6 mm de ancho, dorsifijas, base emarginada, ápice agudo; ovario cónico, 0.7 mm de largo, densamente piloso, placentas 3–4 ovuladas, estilos 3, cilíndricos, glabros, 4.5 mm de largo en flores longistilas; estigma 1.7 mm de largo, penicilado, ca. 10 ramas. Cápsula ovoide, 2–3 mm diám., valvas ovadas, lisas, pilosas por fuera, por dentro lustrosas, castaño claro, vena placentaria prominente. Semilla elipsoide, ligeramente curvada, 1.8 mm de largo, 1.2 mm de ancho, hilo cónico, pequeño, rafe linear, cálaza no prominente, ligeramente cóncava, episperma reticulado, aréolas ± hexagonales; arilo unilateral, ovado, casi tan largo como la semilla, borde eroso, membranáceo y blanquecino en seco.

Esta especie pertenece a la serie *Leiocarpae* Urban por tener pedúnculo floral soldado al pecíolo, pedicelo no desarrollado, estambres soldados en la base al tubo calicino, y frutos lisos. La diferencia en longitud observada entre androceo y gineceo es de 1.7 mm. Es afín a *T. lineata* Urban que se diferencia por tener hojas floríferas no bracteiformes, nectarios con borde piloso, y tubo calicino completamente piloso. También es afín a *T. melochioides* Cambess. var. *arenaria* Urban que se diferencia por sus ramas estigmáticas pilosas en la base y por sus semillas más grandes y curvadas.

Turnera steyermarkii Arbo, sp. nov. TIPO: Venezuela. Territorio Federal Amazonas: Dep. Casiquiare, Río Temi, a lo largo de la orilla derecha del río, aprox. 1–2 horas abajo de Yavita, en sabanita, 100–140 m, 6–19 July 1969, *Bunting, Akkermans & Van Rooden 3671* (holótipo, MY). Figura 3G–K.

Frutex ramosus 1–1.5 m altus. Folia elliptica vel anguste elliptica, obtusa vel subacuta, supra glabra, subtus strigillosa, margine obsolete remoteque crenulato, nervo medio supra impresso strigoso, lateralibus ascendentibus sub angulo 38–60° abeuntibus. Flores verisimiliter heterostyli, pedunculi subnulli, pedicelli nulli, prophylla subspathulata, calyx 2.1–3 mm longus, filamenta pilosa, antherae breves conectivo producto lingulato-apiculato piloso. Semina longitudinaliter striata, dense pilosa.

Arbusto muy ramificado 1–1.5 m de alto, ramas con corteza pardo-negruzca, obscuramente plegado-estriadas, porciones con entrenudos muy cortos alternando con porciones con entrenudos bien desarrollados, cicatrices foliares no salientes; ramas del año estrigosas con pelos muy cortos, simples, adpresos. Hojas con estípulas 0.3 mm de largo, triangulares; yemas seriales no observadas; pecíolo de sección aprox. triangular, aplanado en la cara adaxial, 2–4 mm de largo, estrigoso; lámina coriácea, elíptica o angustielíptica, 40–78 mm de largo, 8–19 mm de ancho, relación largo : ancho = 3–6 : 1, base cuneada o brevemente atenuada, ápice obtuso o subagudo, borde plano o ligeramente revoluto, obscuramente crenulado, con escotaduras remotas, inconspicuas, con 2–3 pares de nectarios diminutos ubicados en las escotaduras basales, haz glabra, verde oscura en vivo, pardo-grisácea en seco, vena media hundida y estrigosa, 8–11 pares de venas laterales apenas visibles o salientes, ángulo de divergencia más frecuente 52° (38–60°), venas terciarias a veces un poco prominentes, envés verde claro en vivo, pardo-rojizo en seco, estrigiloso, pelos cortos estrictamente antrorsos, vena media muy prominente, estrigosa, venas laterales salientes, venación menor conspicua o no. Flores presumiblemente heterostilas (los ejemplares estudiados presentan flores brevistilas), reunidas en espigas breves 10–20 floras, axilares o terminales; brácteas tectrices coriáceas, pecíolo 0.7–1 mm de largo, estrigoso, lámina elíptica, 1.2–2 mm de largo, 0.9–1.2 mm de ancho, ápice agudo, borde entero o denticulado, haz lustrosa, parda, estrigilosa, envés densamente dorado-estrigoso con vena media saliente; pedúnculo nulo o subnulo; profilos 2, insertos en la base del cáliz, subespatulados, 1.5 mm de largo, 0.5 mm de ancho, ápice agudo, cara interna glabra en la base, estrigilosa en el ápice, envés densamente dorado-estrigoso; cáliz 2.1–3 mm de largo, tubo calicino 1 mm de largo, dorado-estrigoso por fuera, cara interna glabra o con algunos pelos en la garganta; corola igual que el cáliz o 0.5 mm más larga, pétalos con la uña soldada al tubo calicino, lámina obovada, 1.2–1.5 mm de largo, 0.5 mm de ancho, base cuneada, pilosa por dentro, ápice agudo; filamentos estaminales 1.6–1.8 mm de largo en flores brevistilas, subulados, pilosos en ambas caras, anteras 0.5 mm de largo,

curvadas a la dehiscencia, base emarginada pilosa, conectivo terminado en un apículo subulado 0.2–0.3 mm de largo, piloso; ovario ovoide, piloso, 0.7–0.8 mm de largo, placentas uniovuladas, estilos 3, cilíndricos, 0.6–0.8 mm de largo en flores brevistilas, hirsutos, terminados en estigmas apenas divididos. Cápsula elipsoide 4 mm de largo, valvas angustielípticas, tuberculadas y estrigosas por fuera, por dentro glabras, rugosas, jaspeadas. Semilla obovoide, 3 mm de largo, 1.8 mm de ancho, longitudinalmente estriada, densamente pilosa, cálaza saliente, cóncava, hilo cónico, rafe linear; arilo unilateral membranáceo, más corto que la semilla.

Material adicional estudiado. BRASIL. AMAZONAS: Rio Curicuriary, afl. Rio Negro, acima da cachoeira, praia baixa perto de Boca do Capanary, 26 Feb. 1936, *Ducke s.n.* (RB).

Turnera steyermarkii es afín a *T. venosa* Urban, que se diferencia por tener hojas agudas y venas laterales con ángulo de divergencia ca. 70°. Urban ubicó esta última especie en la serie *Stenodictyae* con dudas, encontrándola afín también a *T. glaziovii* Urban. *Turnera steyermarkii* y *T. venosa* presentan filamentos estaminales pubérulos y anteras pilosas como *T. serrata* Vell.; tienen flores sésiles reunidas en inflorescencias axilares o terminales, y tienen semillas pilosas como *T. brasiliensis* Willd. ex Schultes y *T. glaziovii* Urban. Como todas estas especies pertenecen a la serie *Salicifoliae* Urban, considero que *T. venosa* y *T. steyermarkii* deben ubicarse en dicha serie y no en la serie *Stenodictyae* Urban.

Dedico esta especie al Dr. Julian A. Steyermark, quien estudió y anotó el ejemplar tipo, marcando sus diferencias con la especie afín, *T. venosa* Urban.

Piriqueta cistoides (L.) Griseb., Fl. Brit. W. I. 298. 1860.

Piriqueta cistoides var. *macrantha* Urban, Jahrb. Königl. Bot. Gart. Berlin 2: 74. 1883. TIPO: Brasil. Bahía: *Martius s.n.* (holótipo, M).

Piriqueta caroliniana var. *exasperata* Urban, Jahrb. Königl. Bot. Gart. Berlin 2: 73. 1883. TIPO: Cuba: *Wright 2609*, plantas 2, 3, y 5 (lectótipo (aquí designado), 5).

Urban (1883) describió *P. cistoides* y *P. caroliniana* con los siguientes caracteres: *P. cistoides* es anual, con flores homostilas, cáliz 4–9 mm de largo, y corola igual o hasta el doble más larga que el cáliz; *P. caroliniana* es perenne, con flores heterostilas, cáliz 6–12 mm de largo, y corola el doble o más larga que el cáliz. El aspecto vegetativo de ambos táxones es muy similar, con la misma variación en tamaño, forma e indumento de hojas, porte y ramificación; su distribución geográfica cubre prácticamente toda el área del género, desde el sur de E.E. U.U. hasta el norte de Argentina.

Los conjuntos de caracteres usados por Urban se encuentran netamente definidos en los extremos del área que ocupan ambos táxones, así en los ejemplares de E.E. U.U. se reconocen los caracteres de *P. caroliniana*, y en los ejemplares de Paraguay y Argentina se reconocen los caracteres de *P. cistoides*. Sin embargo, en el resto del área, desde el Caribe hasta Mato Grosso (Brasil) se encuentran ejemplares de una u otra entidad, y otros cuyos caracteres son intermedios. Ya Urban tropezó con estos ejemplares y describió numerosas variedades; en el ejemplar *Wright 2609* determinó las distintas plantas como *P. cistoides* "var. *genuina*," *P. caroliniana* var. *glabra* y *P. caroliniana* var. *exasperata*. Hay ejemplares de *P. caroliniana* var. *integrifolia* y de *P. cistoides* var. *genuina* que son idénticos excepto en la longitud de androceo y gineceo, y lo mismo ocurre entre *P. caroliniana* var. *caroliniana* y *P. cistoides* var. *latifolia*.

Después de estudiar todo el material disponible (470 ejemplares de numerosos herbarios) y de medir los caracteres cuantitativos, he llegado a la conclusión de que se trata de una sola especie con dos subespecies que muy probablemente se hibridizan en las áreas donde conviven. La mayor parte del material estudiado puede identificarse a subespecie, pero hay ejemplares dudosos, ya sea por su variabilidad o porque presentan caracteres intermedios. Dichos ejemplares, que incluyen algunos tipos, se citan después de las subespecies; los sinónimos citados más arriba son los no identificados a nivel de subespecie.

La combinación *Piriqueta cistoides* Meyer ex Steudel, Nomencl. Bot. 2: 344. 1824, usada por Urban (1883) está basada en *Turnera cistoides* Hort. (non L.), nomen nudum.

Piriqueta cistoides (L.) Griseb. subsp. **cistoides**. *Turnera cistoides* L., Sp. Pl. ed. 2, 1: 387. 1762. *P. cistoides* var. *genuina* Urban, Jahrb. Königl. Bot. Gart. Berlin 2: 74. 1883. TIPO: (holótipo, Linn. Herb. 384. 6).

Piriqueta villosa Aublet, Hist. pl. Guiane 1: 298, t. 117. 1775. *P. cistoides* var. *latifolia* Urban, Jahrb. Königl. Bot. Gart. Berlin 2: 74. 1883. TIPO: Caienne. (holótipo, BM; isótipo, *Herb. J. J. Rousseau*, P).

Turnera aspera Poiret in Lam., Encycl. 8: 141. 1808. TIPO: Caienne, *Poiret herb.* (holótipo, P).

Turnera hirta Willd. ex Schultes in Roemer et Schultes, Syst. veg. 6: 678. 1820. TIPO: *Herb. Willdenow* (holótipo, B n.v., microficha estudiada).

Piriqueta tomentosa Kunth in H. B. & K., Nov. gen. sp. 6. 1823. TIPO: Missiones del Orinoco, inter Atures et Maypures, May, *Humboldt & Bonpland s.n.* (holótipo, P).

Turnera helianthemoides Cambess. in Saint Hilaire A., Fl. Bras. Merid. 2: 224. 1830. *Piriqueta cistoides* var. *micrantha* Urban, Jahrb. Königl. Bot. Gart. Berlin 2: 74. 1883. TIPO: Brasil. Goiás: ad ripas Paranahyba, *Saint Hilaire s.n.* (holótipo, P; isótipo, F).

Piriqueta lanceolata Benth., Hook. J. Bot. 4: 117. 1842. TIPO: Guyana: banks of the Rupunoony, *Schomburgk 127* (holótipo, K; isótipos, BM, FI, P).

Piriqueta foliosa Garcke, Linnaea 27: 63. 1849. *Piriqueta cistoides* var. *foliosa* (Garcke) Urban, Jahrb. Königl. Bot. Gart. Berlin 2: 74. 1883. TIPO: Suriname: ad vias prope plant. Quarta, *Kegel 110* (holótipo, GOET; isótipo, P).

Piriqueta cistoides var. *bracteolata* Urban, Jahrb. Königl. Bot. Gart. Berlin 2: 74. 1883. TIPO: Suriname: *Hostmann 265* (lectótipo (aquí designado), K; isolectótipos, FI, P, W).

Piriqueta cistoides var. *glabrescens* Urban, Jahrb. Königl. Bot. Gart. Berlin 2: 74. 1883. TIPO: Jamaica: *Wullschlaegel 844* (lectótipo (aquí designado), M; isolectótipos, GOET, W).

Todos los ejemplares estudiados de México y Centroamérica y del centro-sureste de Brasil (Minas Gerais, Rio de Janeiro, São Paulo, y Paraná), Paraguay, y norte de Argentina (Formosa) corresponden a esta subespecie. Vive además en numerosas islas del Caribe, Venezuela, Trinidad, las Guayanas, Brasil (Amazonas hasta Mato Grosso do Sul), y Bolivia.

Son plantas generalmente anuales, con raíces típicas cortas y ramificadas; flores de 4–11 mm de largo, relación en longitud corola : cáliz = 1.5 : 1; son homostilas, pero en muchos casos el androceo puede ser hasta 1.5 mm más largo que el gineceo o, a la inversa, el gineceo puede ser hasta 1 mm más largo que el androceo.

Se la ha coleccionado a alturas diversas, desde el nivel del mar hasta los 1,100 m en Cuba.

Material representativo examinado. MÉXICO. TAMAULIPAS: Tampico, Feb. 1839, *Berlandier 62* (MO, P, W). GUATEMALA. PETÉN: Santa Elena, en orillando el camino para La Libertad, km 25, lado E, 24 Apr. 1970, *Tún Ortiz 1020* (F, MO, S). BELIZE: Honey Camp, Sep. 1929, *Lundell 535* (DS, F, K, MO, S). HONDURAS: La Mosquitia, caserío de Rus-Rus, vaguada del Río Rus-Rus, nivel del mar, 17–21 July 1977, *Nelson & Romero 4144* (CTES, MO). NICARAGUA. ZELAYA: Puerto Cabezas, ca. 14°01'N, 83°23'W, ca. 15 m, 3 July 1980, *Stevens 17799* (CTES, MO). CUBA. ISLA DE PINOS: near Nueva Gerona, 12 May 1904, *Curtiss 496* (F, MO, P, US). PUERTO RICO: Dist. Bayamón, Luquillo, Bo. Sabana, 9 Mar. 1938, *Otero 521* (F, MO, US). COLOMBIA. VALLE: Plana del Valle, entre Palmira y Cali, 25 Apr. 1963, *López Figueiras 8457* (US). VENEZUELA. BOLÍVAR: Dist. Piar, Paviche, NW de El Manteco, 215 m, márgenes del lago de Guri, July 1978, *Delascio & Liesner 7165* (MO, VEN). TRINIDAD: St. Augustine, 23 June 1926, *Broadway 6316* (F, MO, S, US). SURINAME: Kwakoegron, 19 Oct. 1944, *Maguire 25006* (F, MO, NY). BRASIL. MINAS GERAIS: na margem do Paranahyba, July 1892, *Ule 163* (HBG, P, RB). BOLIVIA. BENI: Prov. Vaca Diez, Guayaramerin, 65°22'W, 10°49'S, 18 Apr. 1979, *Krapovickas & Schinini 35096* (CTES). PARAGUAY. AMAMBAY: Sierra de Amambay in campis humidis Esperanza, Nov. 1907, *Hassler & Rojas 10710* (BM, G, K, LIL, LY, NY, P, S, W). ARGENTINA. FORMOSA: Clorinda a Pilcomayo, km 6, ruta 11, 21 Oct. 1946, *Morel 1496* (CTES, LIL).

Piriqueta cistoides subsp. **caroliniana** (Walter) Arbo, comb. nov. *Waltheria caroliniana* Walter, Fl. Carol. 175. 1788. *Turnera caroliniana* (Walter) S. Watson, Smithsonian Misc. Collect. 15: 391. 1878. *Piriqueta caroliniana* (Walter) Urban, Jahrb. Königl. Bot. Gart. Berlin 2: 71. 1883. TIPO: E.E. U.U. South Carolina: ad ripas fluvii Santee, n.v.

Turnera integrifolia Willd. ex Schultes., Syst. veg. 6: 679. 1820. *Piriqueta caroliniana* var. *integrifolia* (Willd. ex Schultes) Urban, Jahrb. Königl. Bot. Gart. Berlin 2: 72. 1883. TIPO: Herb. *Willdenow 6089* (holótipo, B n.v., microficha estudiada).

Turnera glabra DC, Prodr. 3: 347. 1828. *Piriqueta glabra* (DC) Griseb., Cat. pl. Cub. 285. 1866, non Chapman. TIPO: Santo Domingo, *Bertero s.n.* (holótipo, DC herb. n. v.; isótipos, M, MO, W).

Piriqueta fulva Chapman, Fl. South. U.S. 146. 1860. TIPO: E.E. U.U. Florida: South Florida, *Chapman s.n.* (holótipo, NY; isótipos, MO, P).

Piriqueta glabra Chapman, Fl. South. U.S. 147. 1860. TIPO: E.E. U.U. Florida: South Florida, *Chapman s.n.* (holótipo, NY).

Turnera tomentosa Alph. Wood, Amer. Bot. Fl. 129. 1874. TIPO: E.E. U.U. Florida: n.v.

Piriqueta tomentosa auct. non Kunth.

Piriqueta caroliniana var. *jacobinae* Urban, Jahrb. Königl. Bot. Gart. Berlin 2: 73. 1883. TIPO: Brasil. Bahía: Serra Jacobina, *Blanchet 2708* (lectótipo (aquí designado), P; isolectótipos, BR, NY, P, W).

Piriqueta cistoides var. *ramosissima* Urban, Jahrb. Königl. Bot. Gart. Berlin 2: 74. 1883. TIPO: Brasil. Goiás: between Funil et São João, *Burchell 9082* (lectótipo, P; isolectótipos, K, NY, P).

Piriqueta viridis Small, Fl. s.e. U.S. 794, 1335. 1903. TIPO: E.E. U.U. Florida: vicinity of Eustis, Lake Co., 16–31 May 1894, *Nash 830a* (holótipo, NY).

Piriqueta tracyi Gand., Bull. Soc. Bot. France 45: 27. 1918. TIPO: E.E. U.U. Florida: Sanibel Island, 17 May 1901, *Tracy 7459* (holótipo, LY; isótipo, F).

Todos los ejemplares de E.E. U.U. corresponden a esta subespecie: son plantas generalmente perennes, con órganos subterráneos ligeramente engrosados, a veces retorcidos en tirabuzón; las flores son grandes, 10–20 mm de largo, y la relación corola : cáliz = 2 : 1; en flores brevistilas el androceo es 2–5 mm más largo que el gineceo, y en flores longistilas el gineceo es 1.5–5 mm mayor; las anteras son ligeramente más grandes que en la subsp. *cistoides*, y los estigmas están mejor de-

sarrollados. Vive además en Venezuela, Colombia, Brasil (Piauí y Bahía hasta Mato Grosso do Sul), Bolivia, y las islas del Caribe. Se la ha coleccionado en lugares bajos, a nivel del mar, y hasta los 800 m en Goiás, Brasil.

Material representativo examinado. E.E. U.U. SOUTH CAROLINA: Bluffton, Beaufort Dist., 1884, *Mellichamp s.n.* (F, K, MO, NY, US). CUBA: Pinar del Río city, at Laguna del Hunco, 30 Oct. 1923, *Ekman 17860* (S). REPÚBLICA DOMINICANA. TRUJILLO: between Bayaguana and Guerra, 8 Nov. 1946, *Howard 9902* (S, US). COLOMBIA. VAUPÉS: San José del Guaviare, 240 m, 11 Nov. 1939, *Cuatrecasas 7645* (F). VENEZUELA. BOLÍVAR: Bajo Caura, sabana Guayapo, 120 m, 2 May 1939, *Williams 12025* (F, S, VEN). BRASIL. BAHÍA: basin on the upper São Francisco river, ca. 26 km NE of Bom Jesus da Lapa on the road to Calderao, ca. 500 m, 43°13′W, 13°09′S, 17 Apr. 1980, *Harley et al. 21443* (CTES). MATO GROSSO: W of km 229, Xavantina–Cachimbo road, 20 Dec. 1967, *Philcox et al. 3628* (K, MO, P, RB).

MATERIAL DUDOSO

Hay ejemplares dudosos de Cuba, República Dominicana, Venezuela, Guayanas, Perú, y Brasil (Amazonas a Mato Grosso do Sul). Este material representa el 10% del total estudiado:

Material representativo examinado. CUBA. PINAR DEL RÍO: San Gabriel to Pinal de La Catalina, 18 Jan. 1912, *Shafer 1844* (F, MO). REPÚBLICA DOMINICANA. Pacificador: Pimentel, 20–25 Jan. 1921, *Abbott 678* (US). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: between Esmeralda and Esmeralda Ridge, in Esmeralda savana, near Orinoco River, 150 m, 21 Aug. 1944, *Steyermark 57772* (F, MO, NY, US). GUYANA: 1837, *Schomburgk 189* (BR, F, K, P). SURINAME: Paramaribo, 8 May 1961, *Hekking 794* (BR, C, MO, NY, P, VEN). PERÚ. SAN MARTÍN: San Roque, 9 May 1925, *Melin 124* (S). BRASIL. AMAZONAS: Río Negro, Manaus, Feb. 1901, *Ule 5403* (HBG, K). MATO GROSSO: 45 km SW de Poconé (Transpantaneira), 56°50′W, 16°25′S, 16 Dec. 1976, *Krapovickas 29936* (CTES, MO).

Piriqueta undulata Urban. Repert. Spec. Nov. Regni Veg. 13: 154. 1914. SÍNTIPOS: Venezuela. Bolívar: Las Botellas, *Passarge & Selwyn 325, 360a, 379, 431* (B, destruidos). NEÓTIPO (aquí designado): Venezuela. Bolívar: Dist. Cedeño, alrededores de Caicara de Orinoco, 200 m, 66°11′W, 07°38′N, 27 June 1981, *Rutkis 354* (VEN; isoneótipo, CTES).

Selecciono esta colección como neótipo porque se encuadra muy bien en la descripción original y procede de un lugar próximo a la localidad típica. El ejemplar de VEN es más completo, con flores y cápsulas bien desarrolladas.

En la publicación original la localidad tipo figura como "Las Botillas." He corregido la ortografía de acuerdo con la obra de Passarge (1933).

LITERATURA CITADA

PASSARGE, S. 1933. Wissenschafliche Ergebnisse einer Reise in Gebiet des Orinoco, Caura und Cuchivero im Jährer 1901–2. Abh. Auslandsk., Reihe C, Naturwiss. 12: 1–281.

STEUDEL, E. G. 1841. Nomencl. bot. ed. 2, 2: 344.

URBAN, I. 1883. Monographie der familie der Turneraceen. Jahrb. Königl. Bot. Gart. Berlin 2: 1–155.

THREE NEW ANDEAN SPECIES OF *AULONEMIA* (POACEAE–BAMBUSOIDEAE)[1]

Lynn G. Clark[2] *and*
Ximena Londoño[3]

ABSTRACT

Three new species of *Aulonemia* are described and illustrated, and comments on the generic limits of *Aulonemia* are included. *Aulonemia longiaristata*, an upper-montane forest species from Ecuador, has large, prominently aristate spikelets. *Aulonemia pumila* is a diminutive páramo species from Colombia, distinguished by its aristate glumes. *Aulonemia robusta*, of upper-montane forests and páramos in Venezuela and Colombia, has robust culms and large, ovate foliage leaves with well-developed fimbriae on the sheath apex and margin. The distribution of each species is mapped, and additional comments on related or similar species are included.

Aulonemia Goudot is a widespread but poorly known bamboo genus of perhaps 30 species, allied to the Arthrostylidiinae (Soderstrom & Ellis, 1987; Soderstrom et al., 1988). It is distributed from southern Mexico through Central America and along the Andes to Peru and Bolivia, with several species known from the Guayana Highlands and central and southeastern Brazil, including the states of Goiás, Minas Gerais, and Espírito Santo south to Rio Grande do Sul. The Andean and Guayanan species usually occur at elevations above 2,000 m, whereas the Brazilian species tend to occur at somewhat lower elevations.

Soderstrom (1988) noted that the vegetative branching of *A. queko* Goudot (the type species of the genus) and *A. hirtula* (Pilger) McClure differs in some respects from that found in other members of *Aulonemia*. Most species of *Aulonemia* exhibit one branch per node, at least on mid-culm and higher nodes, with all the internodes more or less equal in length. In contrast, *A. queko* and *A. hirtula* usually have a series of several short internodes alternating with the long internodes, and a branch complement derived from the basal rebranching of the dominant primary branch. Soderstrom (1988) suggested that these two groups were possibly not congeneric, and that the species with one branch per node were perhaps better accommodated in *Matudacalamus* Maekawa, which McClure (1973) submerged into *Aulonemia*.

Many of the *Matudacalamus*-type species do usually produce only one branch per culm, but we have observed that at least *A. trianae* (Munro) McClure and *A. patula* (Pilger) McClure can produce *Aulonemia*-type branch complements at their lower nodes while producing only one branch per node at the upper nodes. The bulky branch complements of the lower nodes are not usually represented in herbaria, so specimens tend to be misleading as to the potential extent of branch development.

A complete revision of *Aulonemia* is necessary to resolve these morphological and taxonomic questions; for the present, we regard *Matudacalamus* as falling within the limits of *Aulonemia*. The species described in the present paper all appear to be of the *Matudacalamus* type, but we have not verified this in the field for *A. longiaristata*.

During the preparation of these descriptions, we examined material of a number of the Andean species of *Aulonemia*. The morphology and distribution of the fimbriae on the foliage leaf sheaths were especially valuable as vegetative characters in distinguishing species.

Aulonemia longiaristata L. G. Clark & Londoño, sp. nov. TYPE: Ecuador. Azuay: Nudo de Portete, pass between headwaters of the ríos Tarquí (Atlantic) and Girón (Pacific), 9,000 ft., 10 Mar. 1945 (fl), *Camp E-2177* (holo-

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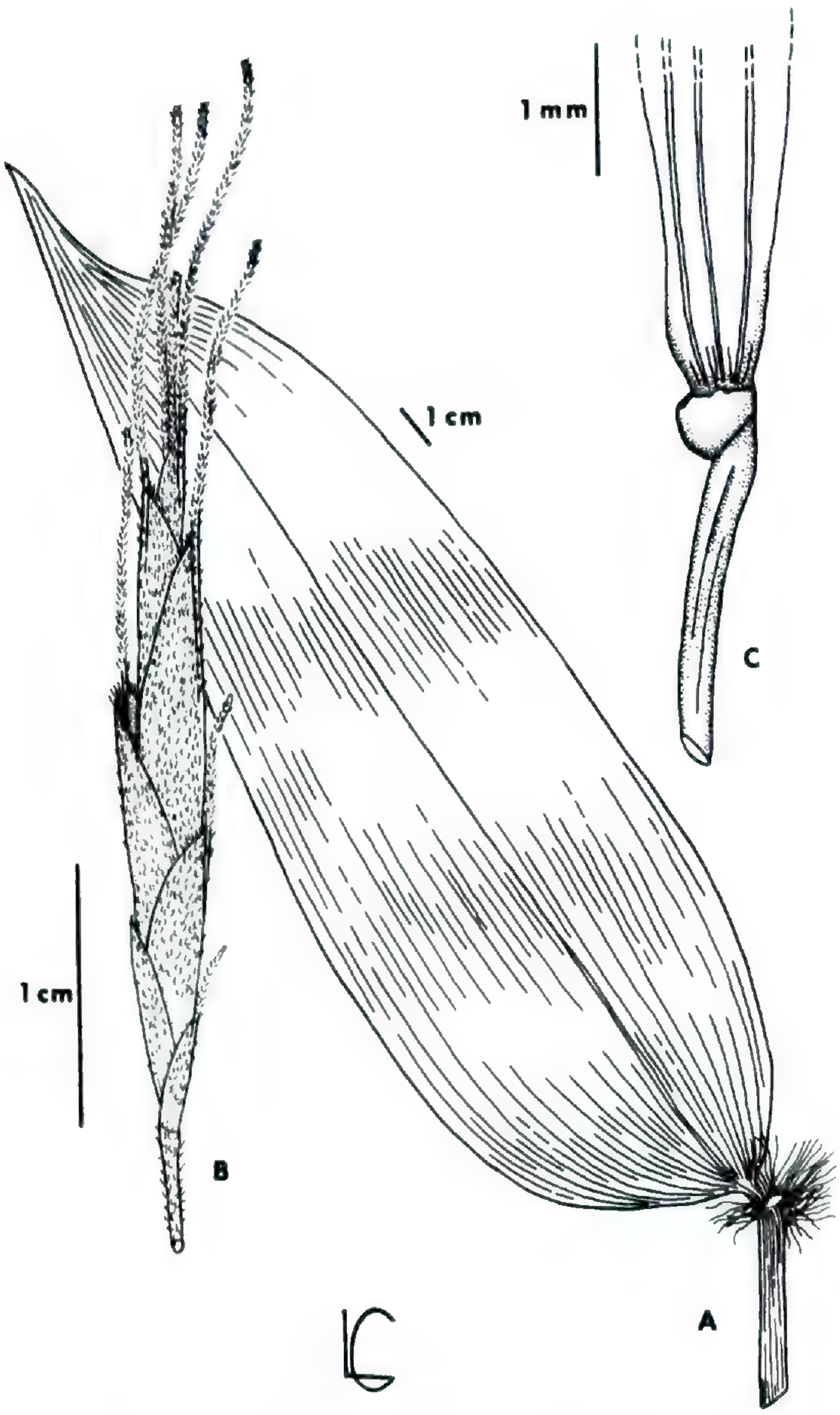

FIGURE 1. *Aulonemia longiaristata.*—A. Foliage leaf and sheath apex with auricle and apical fimbriae.—B. Spikelet.—C. Base of fertile lemma showing the swollen callus. (A based on *Young 128*, B and C based on *Camp E-2177.*)

type, US 2 sheets; isotype, NY). Figures 1, 3.

Culmi usque ad 1.8 cm diametro, 2–4 m alti, erecti. Vaginae foliorum carinatae, glabrae, ad apicem auriculatae, fimbriatae tantum ad apicem, fimbriae 1.5–4 cm longae, plus minusve erectae, scabridae, crispatae; laminae foliorum (11.5–)14–29 cm longae, (1.9–)3.5–10 cm latae, anguste ovatae vel ovatae, reflexae. Inflorescentia paniculata, plus minusve aperta, ad 20 cm longa. Spiculae 2.4–3.4 cm longae arista exclusa, pubescentes, 4–6 flosculos fertiles continentes; lemmata fertilia 10–20.4 mm longa arista exclusa, 9-nervata, arista (4–)9.5–20 mm longa; callus 3–5 mm longus, tumidus, nitidus, flavidus.

Culms to 1.8 cm diam., 2–4 m tall, erect to slightly arching at the tip. *Internodes* to 31 cm long, terete, hollow, smooth. *Culm leaf* sheaths 10.5–13 cm long, 1.9–3 times as long as the blade, apically long-fimbriate, auriculate on one or both sides of the apex; blades 4.4–5.5 cm long, reflexed, pseudopetiolate; girdle 3–7 mm wide, smooth. *Nodes* somewhat swollen; supranodal ridge prominent; branch one per node. *Foliage leaf* sheaths keeled, glabrous, apically auriculate on the side of the overlapping margin (rarely both sides auriculate); fimbriae restricted to the sheath apex, 1.5–4 cm long, ± erect, their basal portions straight, scabrid, their apical portions wavy to curly; blades (11.5–)14–29 cm long, (1.9–)3.5–10 cm wide, narrowly ovate to ovate, reflexed, adaxially glabrous, abaxially glabrous to scabrid, not tessellate, the apex acuminate, the base asymmetrical, one side rounded to rounded-cuneate, the other attenuate to rounded-attenuate; pseudopetiole 0.4–1.2 cm long, pulvinate; outer ligule 0.3–1 mm long; inner ligule 0.5–1 mm long. *Inflorescence* a ± open panicle 14–20 cm long; rachis ± complanate, glabrous; branches angular, the edges scabrous, otherwise glabrous, loosely appressed; pedicels 1–5 cm long, angular, scabrous-pubescent. *Spikelets* 2.4–3.4 cm long excluding awns, pubescent; glume I 6.8–9.5 mm long (including awn), subulate to awned, 3-nerved, the awn to 4 mm long; glume II 10.4–11.2 mm long (including awn), 5- or 7-nerved, the awn 3.7–4.8 mm long; sterile lemma (8.4–)11–13 mm long (excluding awn), 7- or 9-nerved, sometimes enclosing a rudimentary palea, the awn 4.5–5.5 mm long; fertile florets 4–6; disarticulation apparently above the glumes and between the florets, but the florets not separating readily from each other; fertile lemma 10–20.4 mm long (excluding awn), 9-nerved, the awn (4–)9.5–20 mm long, straight to slightly curved, the callus 3–5 mm long, rounded, swollen, shiny, yellowish, prominent in florets at least before anthesis; palea 7.5–11.2 mm long, 2-keeled, acuminate-apiculate, pubescent, 4-nerved, the sulcus broad; rachilla internodes 2.5–5 mm long, finely pubescent, flattened; lodicules not seen; stamens 3, the anthers 5–5.4 mm long; fruit unknown; terminal 1–2 florets rudimentary, 4.8–6 mm long, if two florets then the lower one often awned, and the second awnlike.

Additional specimens examined. ECUADOR. BOLÍVAR: 42 km W of Guaranda on the old road to Babahoyo, *Young 128* (AAU, MO, QCA, US). CHIMBORAZO: Cañon of the Río Chanchan, about 5 km N of Huigra, *Camp E-3393* (NY, US). EL ORO: between Curtincapa and Guagra Uma, 8 mi. NE of Curtincapa on SW slopes leading to Chapel, *Steyermark 53924* (US). IMBABURA: El Tambor, areas de Buenos Aires, Cordillera Occidental, *Acosta-Solis 17218* (US). LOJA: Cariamanga(?), S. Loja, 7 May 1946 (fl), *Espinosa 309* (US).

This species, an Ecuadorian endemic, is named for the long, slender awns of the fertile lemmas. *Aulonemia longiaristata* is also characterized by

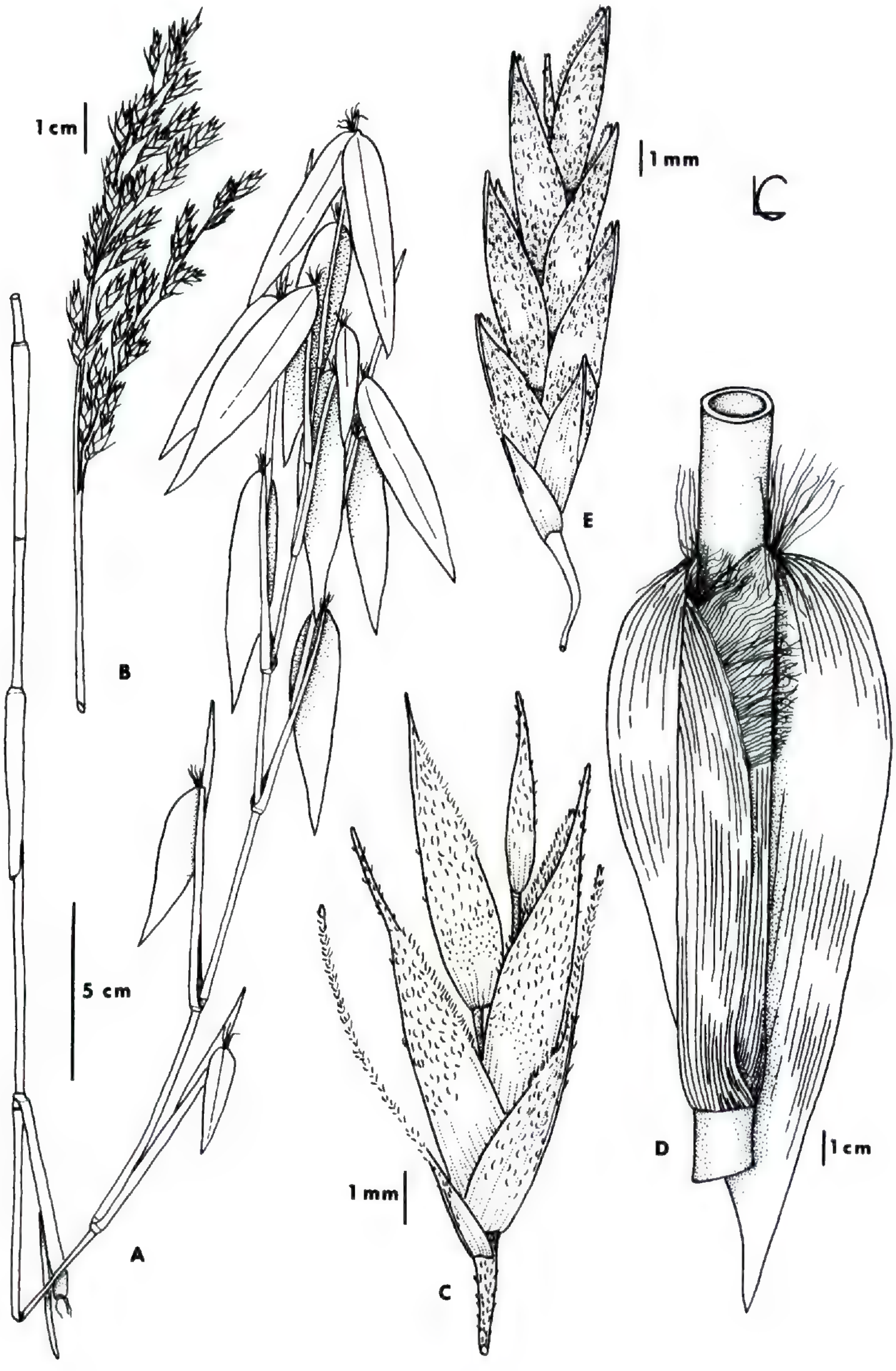

FIGURE 2. *Aulonemia pumila* and *A. robusta*. A–C. *A. pumila*.—A. Habit and branching of culm, with foliage leaves.—B. Inflorescence.—C. Spikelet. (A based on *Londoño et al. 379*, B and C based on *Londoño et al. 382*.) D, E. *A. robusta*.—D. Foliage leaf and sheath apex showing marginal and apical fimbriae.—E. Spikelet. (D based on *Clark & Cavelier 295*, E based on *García-Barriga & Jaramillo M. 19797*.)

its auriculate foliage leaf sheaths with fimbriae restricted to the sheath apex, large foliage leaf blades, pubescent spikelets 2.4–3.4 cm long (excluding awns), and the swollen, rounded callus present at the base of each fertile lemma. According to label data, clumps of *A. longiaristata* form extensive stands in upper montane forest and on ridge tops at elevations of 2,000 to 2,700 m. The plant is called *zadilla* or *carrizo*, and Camp (*E-2177*) noted that its culms were used along with *Arundo donax* L. in the manufacture of baskets and other items.

Aulonemia longiaristata has been confused with another high-elevation member of the genus, *A. patula*. (*Aulonemia sodiroana* (Hackel) McClure is probably synonymous with *A. patula*.) The two

species are rather similar vegetatively, both having large foliage leaf blades, but *A. patula* lacks the sheath auricles, and in addition to its apical fimbriae also exhibits prominent marginal fimbriae that extend about halfway down the overlapping margin of the leaf sheath. The spikelets of *A. patula* may reach 3 cm in length, but usually have seven or eight fertile florets, and the fertile lemmas have short awns usually no more than 4 mm long. A rounded callus is present at the base of each fertile lemma; it is not swollen and prominent as in *A. longiaristata*.

Aulonemia pumila L. G. Clark & Londoño, sp. nov. TYPE: Colombia. Putumayo: km 34 from Pasto on the Pasto–Sibundoy road, Páramo San Antonio del Bordoncillo, 3,210 m, 5 Feb. 1988 (fl), *Londoño & Clark 382* (holotype, COL; isotypes, ISC, MO, NY, TULV, US, WIS). Figures 2A–C, 3.

Culmi 2–3 mm diametro, 0.5–1 m alti, erecti vel procumbentes. Vaginae foliorum parum carinatae, glabrae vel pubescentes, nonauriculatae, fimbriatae tantum ad apicem; fimbriae 5–6 mm longae, erectae, glabrae, sinuatae vel crispatae; laminae foliorum 3 7 cm longae, 0.6–1.4 cm latae, anguste ovatae, reflexae. Inflorescentia paniculata, parum contracta, 5.5–11 cm longa. Spiculae 8.4–11.2(-12.6) mm longae, pubescentes, 2–3(–4) flosculos fertiles continentes; lemmata fertilia 5.5–9.2 mm longa, subulata vel subulata-aristata, 5- vel 7-nervata; callus ad 2 mm longus, planus, nitidus.

Rhizomes pachymorph. *Culms* 2–3 mm diam., 0.5–1 m tall, erect to procumbent. *Internodes* 8–10(–18) cm long, terete, hollow but relatively thick-walled, pubescent. *Culm leaf* sheaths 5–5.5 cm long, ca. 7 times as long as the blade, occasionally a few apical fimbriae present, 2–6 mm long, auricles absent; blade 0.8 cm long, reflexed, shortly pseudopetiolate; girdle to 1 mm wide. *Nodes* slightly swollen; supranodal ridge prominent; branch one per node. *Foliage leaf* sheaths slightly keeled toward the apex, glabrous to pubescent, nonauriculate; fimbriae restricted to the sheath apex, 5–6 mm long, erect, fine, smooth, wavy to curly; blades 3–7 cm long, 0.6–1.4 cm wide, narrowly ovate, reflexed, adaxially glabrous, abaxially glabrous to more commonly scabrid-pilose, not tessellate, the apex acuminate, the base rounded; pseudopetiole 1–1.5 mm long, pulvinate; outer ligule 0.2 mm long; inner ligule to 0.5 mm long. *Inflorescence* a somewhat contracted panicle 5.5–11 cm long; rachis ± complanate, pubescent; branches angular, pubescent, ascending to loosely appressed; pedicels 2–9 mm long, angular, pubescent. *Spikelets* 8.4–11.2(–12.6) mm long, pubescent; glume I (4.3–)7.4–8.3 mm long (including awn), 1-nerved; glume II (5.5–)7.5–8.4 mm long (including awn), 3- or 5-nerved; sterile lemma absent; fertile florets 2–3(–4); disarticulation above the glumes and between the florets, but the lowermost floret often not disarticulating; fertile lemma 5.5–9.2 mm long, subulate to subulate-aristate, 5- or 7-nerved, the callus to 2 mm long, flat, lighter, shiny; palea 4.3–6.3 mm long, 2-keeled, acuminate, 4-nerved, the keels ciliate, the sulcus broad, pubescent; rachilla internodes 1.5–2 mm long, finely pubescent, slightly flattened; lodicules not seen; stamens not seen; fruit unknown; terminal floret rudimentary, 2.9–4.3 mm long.

Additional specimens examined. COLOMBIA. CAUCA: Macizo Colombiano, Valle de Las Papas, alrededores de Valencia, 11 Sep.–1 Oct. 1958 (fl), *Idrobo et al. 3820, 3830* (US). PUTUMAYO: alta cuenca del Río Putumayo, filo de la cordillera entre El Encano y Sibundoy, Páramo de San Antonio del Bordoncillo, 4 Jan. 1941 (fl), *Cuatrecasas 11777* (COL, US); lado sur de la Laguna de la Cocha, Páramo de Santa Lucia (nacimiento del Río Alisales), 9 Jan. 1941 (fl), *Cuatrecasas 11874* (COL, US); km 34.5 via Pasto–Mocoa, Páramo San Antonio del Bordoncillo, 3 Mar. 1987 (fl), *Londoño & Quintero 198* (COL, TULV, US); 32–33 km from Pasto on the Pasto–Sibundoy road, Páramo San Antonio del Bordoncillo, *Londoño et al. 379* (COL, ISC, MO, NY, TULV, US).

Aulonemia pumila is one of the smallest members of the genus, hence its specific epithet. It is characterized by delicate culms 2–3 mm in diameter and 0.5–1 m tall; nonauriculate foliage leaf sheaths with a few, erect fimbriae 5–6 mm long restricted to the sheath apex; foliage leaf blades 3–7 cm long and 0.6–1.4 cm wide; ± contracted panicles 5.5–11 cm long; and pubescent spikelets 8.4–11.2(–12.6) mm long with 2–3(–4) fertile florets and distinctly aristate glumes. This species is known only from three marshy páramo areas in southern Colombia at elevations of 2,900 to 3,250 m.

Aulonemia pumila is similar and perhaps related to *A. trianae*, a more widespread Colombian species. *Aulonemia trianae* is distinguished from *A. pumila* by its culms 1–2.5(–6) m tall, apical fimbriae ca. 1 cm long, foliage leaf blades 6–15 cm long and 1–2 cm wide, more open panicles, spikelets 10–17 mm long with 5–6(–8) fertile florets, and acuminate, not aristate, glumes.

Aulonemia robusta L. G. Clark & Londoño, sp. nov. TYPE: Venezuela. Mérida: Dtto. Sucre, via Estanquez–Las Coloradas–El Molino–Canaguá, Páramo Las Coloradas (Páramo La Laguna), 2,800 m, 14 June 1989 (fl), *Clark et al. 533* (holotype, VEN; isotypes, ISC, MO,

NY, US, and Facultad de Ciencias, Universidad de Los Andes, Mérida). Figures 2D–E, 3.

Culmi 1–2.5 cm diametro, 2–4(–5) m alti, erecti. Vaginae foliorum rotundatae, glabrae, interdum farinosae, nonauriculatae, fimbriatae ad apicem et ad marginem in dimidio superiore; fimbriae tenues, glabrae, crispatae, apicales (1–)3–4 cm longae, marginales 1–3 cm longae, pectinatae; laminae foliorum (5–7.5)19–32 cm longae, (1–1.5)5–13.5 cm latae, ovatae, reflexae. Inflorescentia paniculata, aperta, 35–50 cm longa. Spiculae 1.1–1.6 cm longae, pubescentes, 4–7 flosculos fertiles continentes; lemmata fertilia 5.2–6.7 mm longa, acuminato-apiculata, 7- vel 9-nervata; callus ad 2 mm longus, planus, nitidus.

Culms 1–2.5 cm diam., 2–4(–5) m tall, erect. *Internodes* 30–40 cm long, terete, hollow, sometimes farinose. *Culm leaves* often not clearly distinguishable from the foliage leaves especially on nonbranching culms; sheaths 12–12.5 cm long, 1.5–2 times as long as the blade, fimbriae as for foliage leaves, the apical ones 2–3 cm long, the marginal ones 2.5–3 cm long, auricles absent; blades 6–8.5 cm long, reflexed, pseudopetiolate; girdle 3–5 mm wide, smooth. *Nodes* slightly swollen; supranodal ridge prominent; branching restricted to culm apices, usually one branch per node. *Foliage leaf* sheaths rounded on the back, not at all keeled, glabrous, frequently farinose, nonauriculate; fimbriae fine, smooth, their basal portions straight, their apical portions wavy to curly, the apical fimbriae (1–)3–4 cm long and ± erect, the marginal fimbriae 1–3 cm long, pectinate, extending about halfway down the overlapping margin; blades (5–7.5)19–32 cm long, (1–1.5)5–13.5 cm wide, ovate, reflexed, adaxially glabrous, abaxially retrorsely scabrid, not tessellate, the apex acuminate, the base rounded; pseudopetiole 5–7 mm long, ± pulvinate; outer ligule 1 mm long; inner ligule 2–8 mm long. *Inflorescence* an open panicle 35–50 cm long; rachis ± angular, smooth, mottled; branches angular, smooth, the primary branches basally pulvinate and diverging from the rachis; pedicels 2–10 mm long, angular, smooth, often somewhat sinuous. *Spikelets* 1.1–1.6 cm long, pubescent; glume I 2.5–4 mm long, subulate, abaxially glabrous, 3-nerved; glume II 4–4.7 mm long, acuminate, abaxially with a few scattered hairs toward the apex, 5- or 7-nerved; sterile lemma absent; fertile florets 4–7; disarticulation above the glumes and between the florets, often the lower 1–2 florets tardily or not disarticulating; fertile lemma 5.2–6.7 mm long, acuminate-apiculate, abaxially pubescent, 7- or 9-nerved, the callus to 2 mm long, flat, distinct, lighter, shiny; palea 5.3–6.4 mm long, 2-keeled, acuminate-apiculate, 2-nerved, the sulcus broad, pubescent; rachilla internodes 1.5–2 mm long, glabrous to pubescent, slightly flattened;

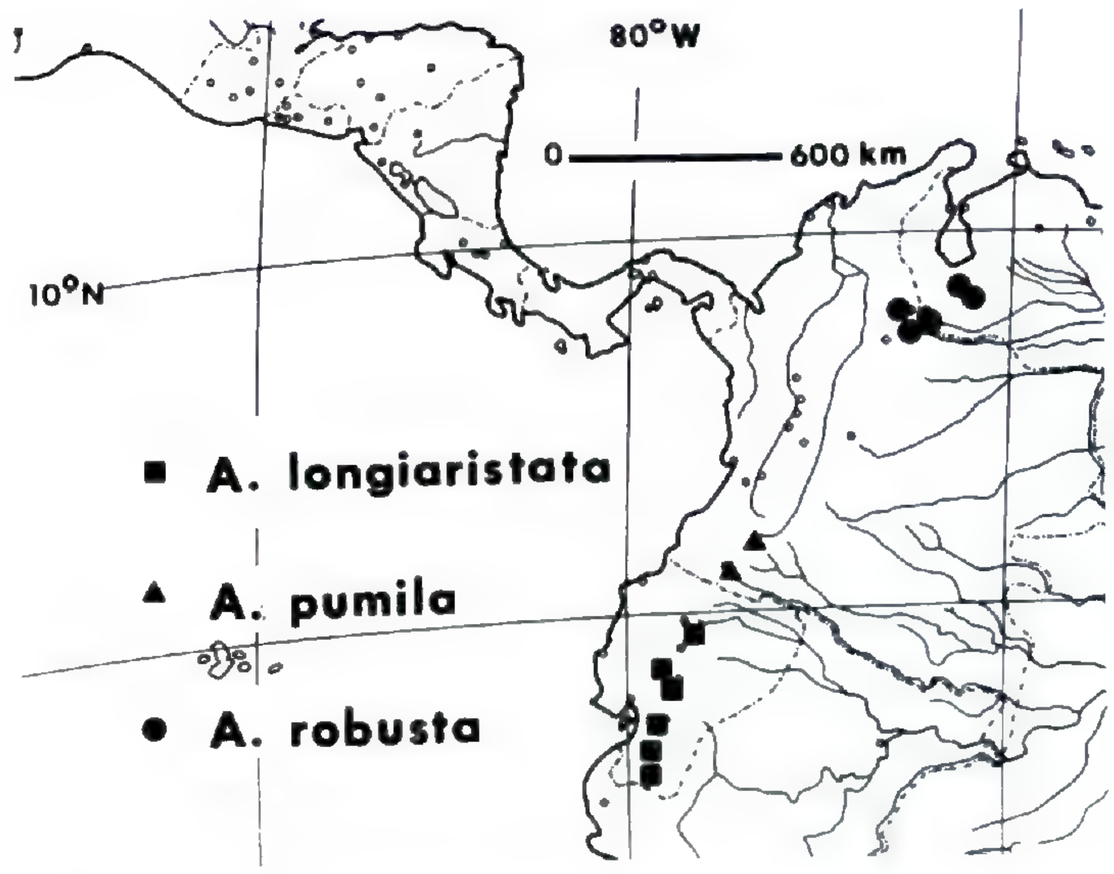

FIGURE 3. Distributions of *Aulonemia longiaristata*, *A. pumila*, and *A. robusta*.

lodicules 3, apically short ciliate, the posterior to 0.9 mm long, the anterior pair 1.1–1.2 mm long, fleshy at the base; stamens not seen; fruit unknown; terminal floret rudimentary, to 2.5 mm long.

Additional specimens examined. COLOMBIA. NORTE DE SANTANDER: Bucaramanga–Pamplona road, between km 108 & 109, *Clark & Cavelier 295* (COL, ISC, MO, US). NORTE DE SANTANDER/CÉSAR: 20 km al sur de Abrego, Las Jurisdicciones (Cerro de Oroque), 19/21 May 1969 (fl), *García-Barriga & Jaramillo M. 19797* (US). SANTANDER: Mpio. Floridablanca/Piedecuesta, via Bucaramanga–Berlin–Pamplona, km 41 between Bucaramanga and Berlin, *Londoño & Clark 477* (COL, ISC, MO, NY, TULV, UIS, US); Mpio. Guaca, via Berlin–Baraya, descending toward Baraya, *Londoño & Clark 481* (COL, ISC, MO, TULV, UIS, US); Mpio. Tona, Santa Rita por la carretera de Bucaramanga a Pamplona antes del Páramo de Berlin, *Murillo & Jaramillo 1217* (COL). VENEZUELA. BARINAS: Dtto. Pedraza, Páramo El Toro, region noreste Los Arbolitos, *Briceño et al. 2329* (Facultad de Ciencias, ULA, Mérida). MÉRIDA: Dtto. Libertador, Páramo El Portachuelo, *Briceño & Adamo 1956* (ISC, Facultad de Ciencias, ULA, Mérida); Dtto. Andres Bello, Páramo El Tambor, 25 Oct. 1985 (fl), *Briceño et al. 1443* (ISC, Facultad de Ciencias, ULA, Mérida); Estanquez-Molino road, Páramo Las Coloradas, *Clark et al. 252* (US, Facultad de Ciencias, ULA, Mérida); Dtto. Campo Elias, El Canalón, entre Manzano Alto y El Campamano, Páramo Los Conejos, Sierra de la Culata, 1 Apr. 1972 (fl), *Ruiz-Teran 7165* (MERF); en las selvas de El Valle (Mucurí) cerca de Mérida, *Vareschi et al. 1760* (VEN). TACHIRA: faldas inmediatamente debajo del Páramo de Tamá, cerca de la frontera Colombo–Venezolano, *Steyermark et al. 98540* (MY, US, VEN); entre el Páramo de Pata de Judío y el Páramo de Cobre, en las laderas conduciendas a la fila de Tierra Negra, cabeceras del Río Quinimarí, 20 km al sur de San Vicente de la Revancha, 16 Jan. 1968 (fl), *Steyermark et al. 101052* (COL, F, NY, US, VEN).

Aulonemia robusta is named for its overall robust appearance, including the stout culms and large leaves. This species is characterized by the

culms 1–2.5 cm diam. and 2–4(–5) m tall with branching restricted to the apices; nonauriculate foliage leaf sheaths with fine, smooth fimbriae 1–4 cm long distributed at the sheath apex and halfway down the overlapping margin; ovate foliage leaf blades 19–32 cm long and 5–13.5 cm wide; and pubescent spikelets 1.1–1.6 cm long with 4–7 fertile florets. *Aulonemia robusta* occurs at elevations of 2,500–3,200 m in upper montane forest, subpáramo, and páramo vegetation in southwestern Venezuela and northeastern Colombia.

Vegetatively, *A. robusta* resembles *A. subpectinata* (O. Kuntze) McClure, a species known only from the Coastal Range of Venezuela. Although comparable in culm height and diameter to *A. robusta*, *A. subpectinata* has narrowly ovate foliage leaf blades 9.3–22 cm long and 2–5.7 cm wide. *Aulonemia subpectinata* also exhibits both apical and marginal fimbriae, but they only reach 3 cm in length, and the basal portion of the fimbriae is flattened and thickened, while the apical portion is narrow, threadlike, and curly. In addition, the spikelets of *A. subpectinata* are (1.2–)2.4–3.6(–4.6) cm long with (5–)6–8(9–11) florets per spikelet.

The spikelets of *A. robusta* are very similar to those of *A. trianae*, but *A. robusta* has much larger inflorescences and is distinguished by its large, ovate foliage leaves and the well-developed apical and marginal fimbriae on the foliage leaf sheaths. The foliage leaves produced on the apical branches of culms of *A. robusta* are often much smaller than the foliage leaves of the main culms, and may be easily confused with those of *A. trianae*. However, the pattern of fimbriae development in *A. robusta* is much different from that of *A. trianae*, which usually has only sparse, apical fimbriae 1 cm long.

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DEVIA XEROMORPHA, A NEW GENUS AND SPECIES OF IRIDACEAE–IXIOIDEAE FROM THE CAPE PROVINCE, SOUTH AFRICA[1]

Peter Goldblatt[2] *and John C. Manning*[3]

ABSTRACT

Devia xeromorpha, a new genus and species of Iridaceae–Ixioideae, is a local endemic of the Roggeveld Escarpment in the western Karoo, South Africa. The new taxon is probably most closely related to the southern and tropical African *Crocosmia*, a member of subtribe Tritoniinae of Ixioideae–Ixieae. *Devia xeromorpha* is remarkable in the Tritoniinae in its narrow, four-grooved leaves; dusty pink, actinomorphic flowers with helically rotated anthers; and tussock-forming habit. The foliar marginal epidermal cells are heavily thickened, and submarginal sclerenchyma is absent; the bundle caps are strongly developed and reach to the epidermis; and stomata are restricted to the laminar grooves. The seed coat of *Devia* is of the basic type for Iridaceae in its brown, microreticulate outer surface. Basic chromosome number for Tritoniinae is $x = 11$ but *Chasmanthe* and some species of *Tritonia* have $n = 10$. *Devia*, with $n = 10$, is consistent with this pattern, but it differs from *Crocosmia* which has the basic number for the subtribe. Although some of the differences between *Devia* and *Crocosmia* reflect xeromorphic adaptations in the former (persistent tunics, proteranthous and peculiar fibrotic leaves), the genus appears to have followed an independent evolutionary pathway, becoming specialized in the structure of the leaf and in orientation of the stamens and style.

A new species of Iridaceae subfamily Ixioideae, discovered by the first author in 1981 in fruit on the Roggeveld Escarpment in the western Karoo of the Cape Province, South Africa, was collected in full flower in January 1989. The ample material that is now available makes it clear that the plant is not only a new species but also that it does not accord with any genus of Iridaceae so far described. The species is assigned to a new genus, *Devia*, named in honor of Dr. M. P. de Vos, of Stellenbosch, South Africa, in recognition of her extensive systematic, anatomical, and embryological research in Iridaceae and other families of southern African plants.

Devia (Fig. 1) is characterized by large, persistent corms with tough long-lived fibrous corm tunics; a branched spike of numerous, small actinomorphic flowers; small membranous bracts; a style with short, apically notched branches; helically rotated stamens; and globose capsules with one or two large seeds per locule. The leaves are unusual in both their structure and phenology. They are heavily fibrous and have two large grooves running the length of each surface, between the central (pseudomidrib) and secondary veins. The leaves are proteranthous and are quite dry by anthesis, and their persistent bases accumulate for years in a thick fibrous mass around the base of the plants. Vegetative increase in the number of corms results in a clumped habit, and the plants sometimes grow in dense concentrations among low shrubs or on open slopes.

LEAF ANATOMY

The leaves of *Devia* are unusual in Ixioideae, although they conform to the basic isobilateral (equitant) type for the family. The central veins are heavily thickened, and deep grooves run the length of both surfaces between the pseudomidrib and secondary veins (Figs. 1K, 2A). There is also a pair of shallow grooves between the margin and secondary veins. A formal anatomical description follows.

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FIGURE 1. Habit, reproductive morphology, and leaf anatomy of *Devia xeromorpha* (*Snijman & Manning 1194*).—A. Habit, ×0.5.—B. Flowering spike, full size.—C. Corm, ×0.67.—D. Side and top view of flower, ×2.—

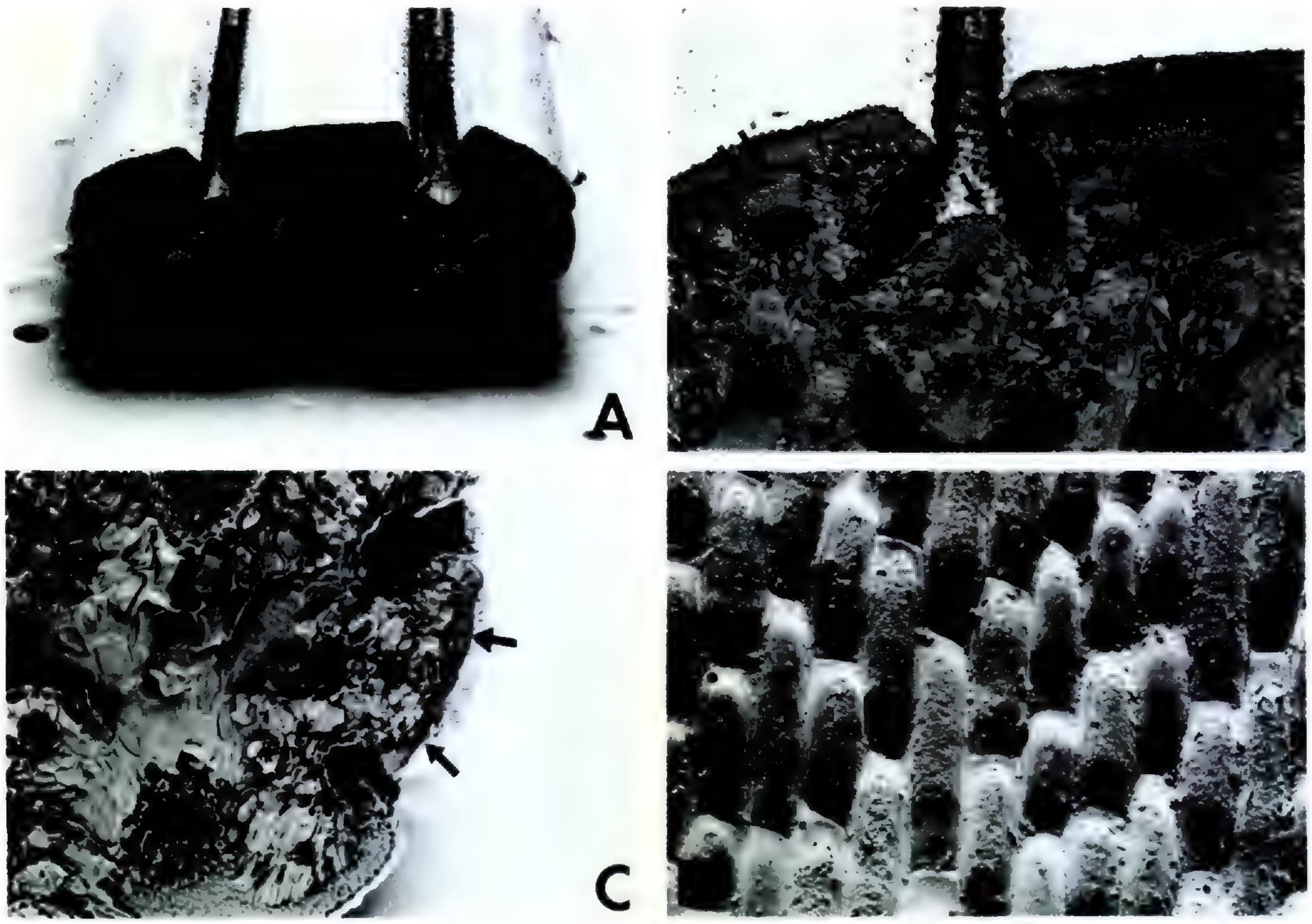

FIGURE 2. Scanning electron micrographs of critical-point dried leaves of *Devia xeromorpha* (*Snijman & Manning 1194*).—A. Leaf transection, ×25.—B. Laminar groove showing papillate ridge (single arrow) and vascular girders (double arrow) ×60.—C. Leaf margin showing thickened marginal palisade epidermis (arrowed), ×100.—D. Leaf surface, without stomata, showing elongate, epapillate epidermal cells.

LEAF TRANSVERSE SECTION

Blade isobilateral, monofacial, more or less oblong, with large paired, opposed grooves (sinuses) between the median and submarginal vein pairs (Fig. 2A–C), the sinuses with low median ridges, and with a pair of smaller shallow sinuses (Fig. 1K) without median ridges between the submarginal and marginal veins. *Cuticle* thick and domed over the cells, but thin within the sinuses. *Epidermis* cells wider than high, outer walls thickened and minutely denticulate in those along the ribs; cells 2–4 times longer than wide in surface view, without papillae (Fig. 2D); marginal cells palisade, heavily thickened (Fig. 2C), especially on the anticlinal walls; long papillae on the cells on the lips of the sinuses and on the ridges within the larger sinuses (Fig. 2B). *Stomata* restricted to the sinuses, sunken; guard cells with a slight outer cuticular lip, much smaller than the neighboring epidermal cells, which overarch them. *Vascular bundles* in two opposite rows, highly variable in size: primary vascular bundles median (forming the pseudomidrib); secondary bundles submarginal; tertiary bundles single below each margin and also in two opposed pairs, between the primary and secondary bundles (below the sinus ridges); 2–6 quarternary or minor bundles alternating with the others, and one centripetal to each marginal tertiary bundle. Xylem pole oriented to the interior except in the marginal tertiary bundle, which is bicollateral and oriented at right angles to the rest. The xylem and phloem poles in the primary and secondary bundles separated by two layers of parenchymatous cells. *Outer sheath* of bundle sheaths a continuous layer of sclerenchyma in primary and secondary bundles, extending as T-shaped girders to the epidermis, the crossbars three or four cells thick, reaching to the edges of the ridges; outer sheath also extending as a sclerenchymatous girder to the epidermis from the submarginal tertiary bundles (Fig. 2B); inner sheath sclerenchymatous as a complete sheath in primary

←

E. Bracts, ×3.—F. Dissected flower with ovary and style, ×3.—G. Anthers, ×4.—H. Apex of style and style branches, ×7.—I. Capsules, full size.—J. Seeds, ×5.—K. Leaf transection (small submarginal sinuses arrowed), ×20.

and secondary bundles, forming bundle caps only in tertiary bundles. *Chlorenchyma* forming broad bands surrounding the sinuses, about eight rows deep, cells at most slightly elongated. *Central ground tissue* of large loosely packed parenchymatous cells, separated from chlorenchyma by an incomplete band of tanniniferous cells one or two cells wide; tanniferous cells also present sporadically in the chlorenchyma and outer sheath of marginal tertiary or quarternary vascular bundles.

Chromosome Cytology

A diploid chromosome number of $2n = 20$ was determined from mitosis in root tips harvested from sprouting corms. The root tips were pretreated in hydroxyquinoline and squashed after hydrolysis in FLP orcein following a technique outlined elsewhere (Goldblatt, 1980, 1981). The chromosomes are relatively small, 2–3 μm long, and range from acro- to submetacentric. Two slightly longer chromosome pairs can be distinguished, and a pair of small satellites is located on the short arm of one of the short chromosome pairs. The chromosomes are comparable in size to those of most genera of Ixioideae (Goldblatt, 1971). The karyotype matches closely those described for *Ixia* and *Dierama* ($x = 10$) in number and appearance of the chromosomes and with *Tritonia* and *Crocosmia* ($x = 11$) in general appearance (Goldblatt, 1971; de Vos, 1982a).

Relationships

The affinities of *Devia* are most likely with *Tritonia*, *Crocosmia*, and *Chasmanthe* (Ixieae–Tritoniinae sensu Goldblatt, 1971). *Devia* shares with most species of these genera a leaf structure in which the marginal epidermis is heavily thickened and not associated with submarginal sclerenchyma, while the laminar bundles have thick sclerenchyma caps often extending to the epidermis as girders (cf. de Vos, 1982b, 1984). This type of leaf anatomy is uncommon in Ixioideae but is also found in *Sparaxis*, *Synnotia*, *Freesia*, *Anomatheca*, *Tritoniopsis*, and *Anapalina* (unpublished).

Devia shares with *Crocosmia* and *Chasmanthe* rounded, hard-walled capsules containing few seeds, up to two per locule in *Devia*, and short, apically stigmatic and sometimes bifurcate style branches; and with *Crocosmia* alone, a persistent corm. *Tritonia* has many-seeded capsules, smaller and usually angular seeds, and typically obovoid capsules. *Devia* differs from both *Crocosmia* and *Chasmanthe* in several significant features. The leaves of *Devia* are unique in Tritoniinae in having paired longitudinal grooves, although this is a common xeromorphic feature of several genera of other subtribes of Ixioideae (e.g., *Gladiolus* spp., *Geissorhiza* spp., and most notably, *Romulea*). The flowers are actinomorphic but with spirally rotated stamens and an eccentric style. Species of *Crocosmia* and *Chasmanthe* (de Vos, 1984, 1985) are mesomorphic and have broad, soft-textured leaves, either plane or plicate, and with the exception of *Crocosmia aurea* Planchon, zygomorphic flowers. In *Crocosmia* and *Chasmanthe* but not *Tritonia* the pseudomidrib consists of several pairs of vascular bundles (de Vos, 1984, 1985). Perianth color in *Crocosmia* and *Chasmanthe* is orange to red (yellow in one variant of *Chasmanthe floribunda* (Salisb.) N.E.Br.), which also contrasts with the dusty pink perianth of *Devia*. The stamens in *Crocosmia* and *Chasmanthe* are never spirally rotated, but are either unilateral and arched below the upper tepal in zygomorphic-flowered species or straight and surrounding the central style in actinomorphic-flowered *Crocosmia aurea*.

The diploid chromosome number in *Devia*, $2n = 20$, corresponds with that of *Chasmanthe* ($x = 10$) but not with *Crocosmia* ($x = 11$) (Goldblatt, 1971; de Vos, 1984).

Devia is probably most closely allied to *Crocosmia*, yet in addition to the differences discussed above, the seeds of *Crocosmia* have a thick hydrophilic coat (possibly an adaptation for bird dispersal) that becomes loose on dehydration and then can be abraded easily (de Vos, 1982b). The seed coat of *Devia* appears to be of the basic type for Iridaceae, having a brown, microreticulate outer surface.

Although some of the differences between *Devia* and *Crocosmia* reflect xeromorphic adaptations in the former (persistent tunics, proteranthous and peculiar fibrotic leaves), the genus appears to have followed an independent evolutionary pathway and become specialized in the structure of the leaf and orientation of the stamens and style.

Systematics

Devia xeromorpha Goldbl. & Manning, gen. et sp. nov. TYPE: South Africa. Cape: Roggeveld Escarpment, farm Vierfontein, NW of Sutherland, rocky loam in renosterveld, *Snijman & Manning 1194* (holotype, NBG; isotypes, K, MO, PRE, S, STE, WAG). Figures 1–3.

Plantae 50–70 cm altae, cormo globoso 2–2.7 cm diam., persistentis, tunicis fibrosis, foliis siccis sub anthesi linearibus 35–45 cm longis 2.5 mm latis, inflorescentia

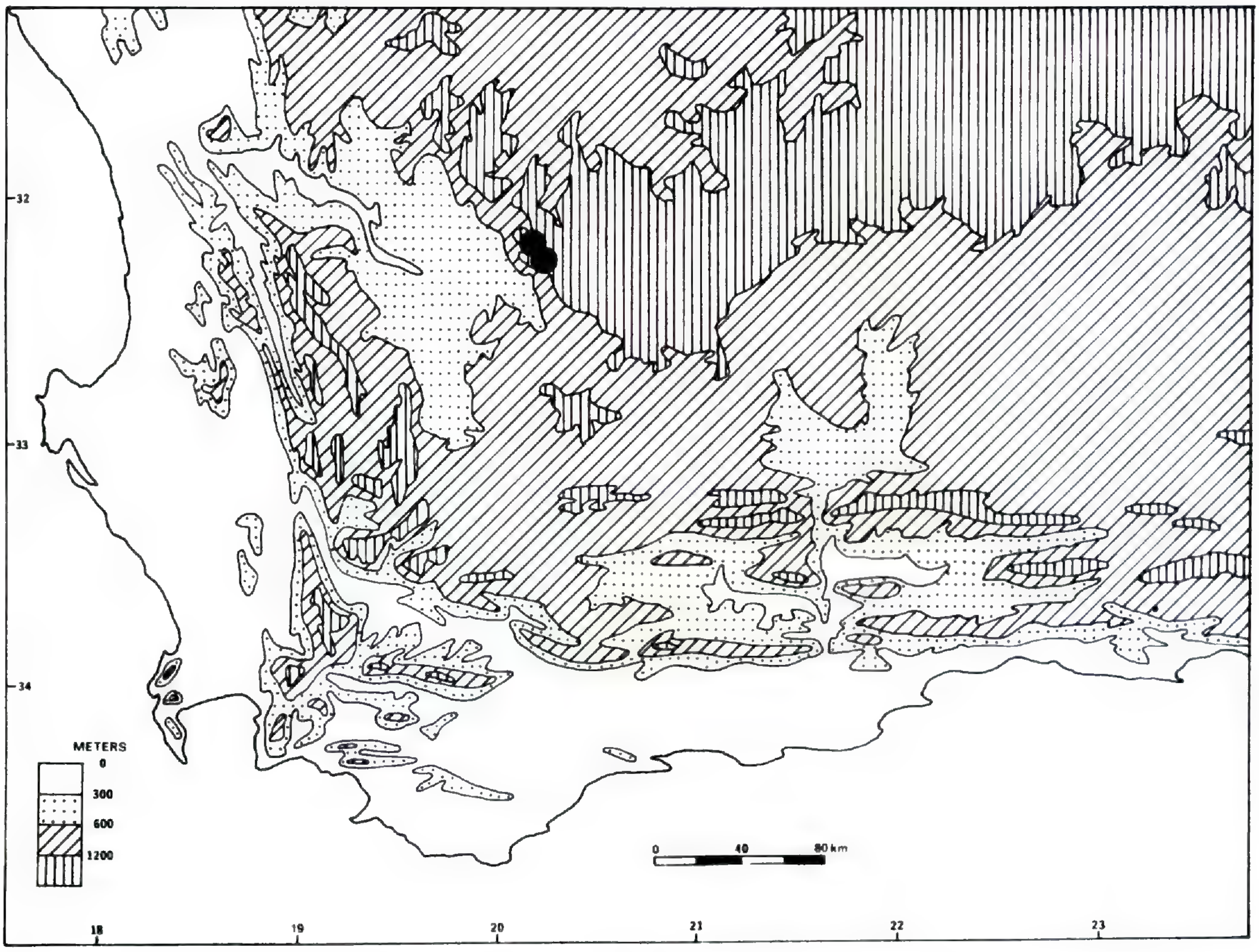

FIGURE 3. Southwest portion of southern Africa showing the distribution of *Devia xeromorpha*.

spica 18–26 florum secunda, floribus actinomorphibus roseo-bubalinis, tubo anguste infundibuliformis ca. 9 mm longo, tepalis ovatis ca. 6 mm longis, staminibus helice rotatis, stylo eccentricis, ramis ad apicem furcatis, capsulis globoso-trigonis, seminibus (0)1–2 per loculis, 2–3 angulatis, 3.5–4.5 mm longis.

Plants 50–70 cm high, growing in dense tufts. *Corm* depressed-globose, 5–6 internodes long, 2–2.7 cm diam., surface and inner tissue bright orange, persisting for several years, thus several corms lying above one another; tunics coarsely fibrous, persisting for several years and forming a thick neck around the base. *Cataphylls* 2, cartilaginous, pale or becoming dry and brown, especially above the ground, the inner largest and reaching 2–4 cm above the ground, sheathing the leaves initially, later decaying. *Leaves* dry at anthesis, usually 6, linear, 35–45 cm long, 2.5 mm wide, tapering gradually to a pungent apex, narrowly oval in section with the central vein area heavily thickened, and with 2 narrow grooves running the length of each surface. *Stem* (0)1–3-branched, sheathed entirely by 5–6 imbricate bracts, these dry by anthesis. *Inflorescence* a spike, the main axis bearing 18–26 flowers, the lateral spikes with 5–10 flowers, secund, axes ascending; *bracts* paired and opposed, dry-membranous, 2.5–4 mm long, translucent at the edges, minutely brown-speckled toward the center and base, the outer bracts enclosing the inner ones and acute, the inner bracts about as long as the outer ones but forked apically. *Flowers* actinomorphic, dusty dull pink, odorless, the style eccentric; *perianth tube* narrowly funnel-shaped, ca. 9 mm long, the lower cylindric part 5–6 mm long, straight or curving upward; *tepals* ascending, ovate, ca. 6 mm long, ca. 3.5 mm wide. *Filaments* inserted at the base of the upper part of the tube, rotated counterclockwise the width of one tepal, ca. 9 mm long, thus reaching to the tepal apices; *anthers* opposite the inner tepals, longitudinally dehiscent, sub-basifixed, thecae separate in the lower quarter, linear, ca. 4 mm long, yellow. *Ovary* obovoid, ca. 1.8 mm long, *style* ca. 16 mm long, reaching to about mid anther level, branches ca. 0.5 mm long, bifid, stigmatic only at the apices. *Capsules* globose-trigonous, 5–6 mm high, 6–8 mm wide, cartilaginous, hard when dry, pale straw-colored, lightly verrucose toward the

apex; *seeds* (0)1–2 per locule, dark brown, 2–3-angled, surface microreticulate, 3.5–4.5 mm long, ca. 3 mm at the widest, funicle whitish, often persisting, lightly adhering to the raphe. *Chromosome number* $2n = 20$.

Flowering time. December and January.

Distribution and habitat. *Devia xeromorpha* is restricted to the highest parts of the Roggeveld Escarpment in the western Karoo (Fig. 3). Extensive populations occur northwest of Sutherland in the vicinity of Sneeukrans on several farms that extend along the steep escarpment edge. The elevation in this part of the escarpment is 4,800–5,600 ft. (1,100–1,300 m), and the area receives slightly higher precipitation than the surrounding, somewhat lower country. The escarpment extends for a considerable distance to the north, almost as far as Calvinia, and it seems likely that *Devia* may occur elsewhere along the escarpment in areas of higher elevation and precipitation, but it has yet to be recorded except close to Sneeukrans. The leaves emerge in March in early autumn and grow throughout the winter and spring, the wettest period in the Roggeveld. They begin to dry out in November and are usually dead at flowering time, which occurs in summer, normally the dry season here.

Several individuals of a small species of long-tongued fly in the Bombyliidae were observed visiting and probing the flowers of *Devia* in the mid-morning, and may be the pollinator.

Additional specimens examined. SOUTH AFRICA. CAPE: 32.20 (Sutherland) Uitkyk farm, Roggeveld NW of Sutherland (AD), *Goldblatt 6357* (MO); Sneeukrans, south of Voelfontein, ca. 4,500 ft., *Goldblatt 6343* (MO).

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LEAF AND CORM TUNIC STRUCTURE IN *LAPEIROUSIA* (IRIDACEAE–IXIOIDEAE) IN RELATION TO PHYLOGENY AND INFRAGENERIC CLASSIFICATION[1]

Peter Goldblatt[2] *and John C. Manning*[3]

ABSTRACT

The tropical and southern African *Lapeirousia*, comprising 35 species, divides into two subgenera on the basis of leaf type. Leaf anatomy of eight species of *Lapeirousia* and selected species of the other five genera of Watsonieae was examined and compared with that of the putatively primitive *Pillansia*. *Lapeirousia* subg. *Lapeirousia* has corrugate leaves that lack a distinct midvein and are anatomically specialized in having predominantly or exclusively alternate vascular bundles and square, truncate costal ridges in which the epidermal cells are abruptly enlarged and often heavily thickened in the outer periclinal walls. This derived leaf structure correlates with the specialized woody corm tunics of the subgenus. Subgenus *Paniculata* has plane leaves with a distinct midvein, vascular bundles usually opposite, and rounded costal ridges with epidermal cells gradually diminishing in size and usually without a heavily thickened outer periclinal wall, the basic type for the tribe. Species of subg. *Paniculata* also have hard corm tunics composed of densely compacted fibers, the basic type for the clade including *Lapeirousia*. Several morphological characters within both subgenera of *Lapeirousia* were used in the construction of a cladogram indicating the major lineages in the genus. This forms the basis for our infrageneric classification that recognizes two subgenera, each with two sections.

The 35 species of *Lapeirousia* (Iridaceae–Ixioideae) occur primarily in the winter rainfall zone of southern Africa and in semiarid southwest tropical Africa, but a few species are widespread across sub-Saharan Africa. Based on its forked style branches and the absence of flavone *O*-glycosides, *Lapeirousia* was assigned to Watsonieae, one of three tribes of Ixioideae (Goldblatt, 1989, 1990a); Watsonieae also include *Watsonia* (52 species), *Thereianthus* (6 species), *Micranthus* (3 species), and *Savannosiphon* (1 species). All except the last are restricted to southern Africa. Until now relationships among the species of *Lapeirousia* have been obscure, and there has been no phylogenetic analysis of the genus nor any modern attempt to provide an infrageneric classification. Baker's (1892, 1896) recognition of three subgenera no longer has any utility, since his subg. *Anomatheca* is now regarded as a genus of tribe Ixieae. His subgenus *Sophronia* included at most four species and merits at best sectional rank. In this paper we investigate the major differences among the species of *Lapeirousia*, namely the nature of the corm tunics and leaf structure, and use these features to establish a new infrageneric classification. This study has been made in conjunction with a systematic revision of *Lapeirousia* in tropical Africa (Goldblatt, 1990b).

Leaf structure and corm tunic structure vary in an apparently consistent pattern across species in tropical and southern Africa. That these two independent features are correlated suggests a major division in the genus into two groups, for which we propose subgeneric rank. The anatomical basis for the leaf variation is explored here, and we propose a phylogeny for the major species groups in *Lapeirousia* based on several independently varying characters (Table 2). We recognize subg. *Pani-*

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TABLE 1. Leaf anatomical characters for the species studied and voucher data. (*G & M = Goldblatt & Manning.*) All vouchers are housed at MO. Coding for each character is as follows with the primitive condition indicated by 0 and the derived states by 1, 2, or 3.

1. Blade profile transverse section: 0 plane, 1 zigzag, 2 elliptic, 3 elliptic and hollow
2. Pseudomidrib: 0 absent, 1 present
3. Rib profile: 0 rounded, 1 truncate
4. Vascular bundles: 0 opposite, 1 alternate
5. Marginal bundle: 0 absent, 1 present
6. Sclerenchyma bundle sheath: 0 phloem cap, 1 complete
7. Subepidermal marginal sclerenchyma: 0 absent, 1 present
8. Bundle position: 0 all subepidermal, 1 major bundles subepidermal and minor ones embedded
9. Leaf margins: 0 rounded, 1 flanged

Taxon	Number of character state									Voucher data
	1	2	3	4	5	6	7	8	9	
Pillansia										
templemannii L. Bolus	2	0	0	0	0	0	0	0	0	*Powrie s.n.*
Watsonia										
aletroides (Burm. f.) Ker	0	1	0	0	1	0	1	1	0	*Sidey 1754*
laccata (Jacq.) Ker	0	1	0	0	0	0	1	1	0	*Rycroft 2531*
Micranthus										
alopecuroides (L.) Rothm.	3	0	0	0	1	1	0	1	0	*Grant 3489*
Thereianthus										
minutus (Klatt) G. Lewis	0	1	0	0	1	1	0	1	1	*Bolus s.n.*
spicatus (L.) G. Lewis	0	1	0	0	1	1	0	1	1	*Grant 5027*
Lapeirousia subg. *Paniculata*										
Section *Paniculata*										
avasmontana Dinter	1	1	0	1	1	0	0	1	0	*G & M 8798*
bainesii Baker	0	1	0	0	1	0	0	1	0	*G & M 8808*
coerulea Schinz	1	1	0	1	1	0	0	1	0	*G & M 8811A*
gracilis Vaupel	0	1	0	0	1	0	0	1	0	*Seydel 3419*
otaviensis R. Foster	0	1	0	0	1	0	0	1	0	*G & M 8837*
schimperi (Aschers & Klatt) Milne-Redh.	0	1	0	0	1	0	0	1	0	*Grant 4507*
Section *Fastigiata*										
corymbosa (L.) Ker	0	1	0	0	1	1	0	1	0	*Gillett 4503*
Lapeirousia subg. *Lapeirousia*										
Section *Sophronia*										
anceps (L.f.) Ker	1	0	1	1	1	0	0	1	0	*Drège 8507a*
odoratissima Baker	1	0	1	1	1	0	0	1	0	*G & M 8803*
pyramidalis (Lam.) Goldbl.	1	0	1	1	1	0	0	1	0	*Mauve & Oliver 233*
Section *Lapeirousia*										
divaricata Baker	0	1	1	1	1	0	0	1	0	*Goldblatt 2754*
Savannosiphon										
euryphylla (Harms) Goldbl. & Marais	0	0	0	0	1	0	0	0	0	*Pawek 10753*

culata for species with plane leaves having a distinct central vein and with corm tunics composed of densely compacted fibers; subg. *Lapeirousia*, by contrast, is made up of species with corrugate (shallowly plicate) leaves lacking a distinct central vein and having corm tunics of uniformly woody texture.

Inflorescence structure and bract morphology appear to coincide with this division to some extent but the patterns of variation in these two features are complex and sometimes contradictory, indicating a degree of convergence that obscures the major patterns of variation. Our conclusions are presented in the form of a cladogram for which

TABLE 2. Characters used in the cladogram (Fig. 3). The derived (apomorphic) states are listed first followed by the presumed ancestral (plesiomorphic) conditions. Apomorphies for *Savannosiphon* are taken from Goldblatt (1989). Other possible synapomorphies for sect. *Fastigiata* are discussed in the text. Anatomical specializations for *L. corymbosa*, the only species of sect. *Fastigiata* known anatomically, are not included in the cladogram.

1. Corm bases flat—corm bases rounded
2. Corm tunics woody—corms tunics of compacted fibers
3. Margins of corm toothed/spiny—margins of corm not elaborated
4. Leaves corrugate—leaves plane and with a pseudomidrib
5. Major veins alternate—major veins opposite
6. Ribs truncate—ribs rounded
7. Stems angular—stems terete
8. Inflorescence a pseudopanicle—inflorescence a spike
9. Flower zygomorphic—flower actinomorphic
10. Bracts small—bracts relatively large
11. Bracts ± membranous and dry above at anthesis—bracts herbaceous
12. Capsules coriaceous—capsules woody
13. Plants short and inflorescence congested—plants tall and inflorescences not notably congested

the characters are either discussed here or are taken from completed work (Goldblatt, 1989, 1990b, c).

MATERIALS AND METHODS

Leaf sections were prepared by following a standard graded ethanol dehydration and wax embedding technique. Serial sections were mounted on slides and stained in saffranin, sometimes counterstained in fast green, and permanently mounted in Canada balsam. Leaves studied, with a few exceptions, were collected from living plants in the field and fixed in FAA. Leaves taken from herbarium specimens were rehydrated in aerosol OT. One leaf was examined for each of the species studied. Voucher information is cited in Table 1.

The cladogram (Fig. 3), based on the data matrix (Table 3), was constructed without the use of a computer.

CHARACTER ANALYSIS

CORM TUNICS

There are substantive differences between the corm tunics of the two subgenera of *Lapeirousia*. Members of subg. *Lapeirousia* have corms with tunics composed of concentric hard, woody layers with smooth surfaces. With age these layers generally fragment irregularly into smaller pieces but rarely become fibrous or cancellate (Fig. 1A, B). In contrast, the tunics of subg. *Paniculata* are composed of densely compacted layers, which sometimes have a nearly woody texture and decay in a different manner. They fray at the lower edges, breaking into regular vertical strips that become increasingly fibrous with age, and sometimes become distinctly netted above or entirely (Fig. 1C–E). The anatomical basis for the differences is unknown. Within the two subgenera there are differences of lesser significance. In several species of subg. *Lapeirousia* the lower margins of the tunics are ornamented with small teeth, whereas in other species the edges are simply rounded (Goldblatt, 1972). In subg. *Paniculata* the way in which the tunics age is often characteristic of species. Some have tunics that form more or less regular vertical strips at least at the base, but that do not become fibrous, whereas the development of a fibrous texture characterizes others. Based on comparison with the genera closely allied to *Lapeirou-*

TABLE 3. Data matrix for *Savannosiphon* and the major generic clusters of *Lapeirousia*, numbered as in Table 3. Presence of the specialized condition is denoted by x; absence by −.

Genus	Character number												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Savannosiphon	−	−	−	−	−	−	x	−	x	−	−	x	−
Lapeirousia													
Subgenus *Lapeirousia*													
Section *Lapeirousia*	x	x	x	x	x	−	x	−	x	−	−	x	−
Section *Sophronia*	x	x	−	x	x	x	x	−	x	−	−	x	−
Subgenus *Paniculata*													
Section *Paniculata*	x	−	−	−	−	x	x	x	−	x	x	x	−
Section *Fastigiata*	x	−	−	−	−	x	x	x	−	x	−	x	x

FIGURE 1. Representative corm tunics in *Lapeirousia*. Subgenus *Lapeirousia*:—A. *L. plicata* (Jacq.) Diels (*Goldblatt 6052*).—B. *L. dolomitica* Dinter (*Nordenstam & Lundgren 1715*). Subgenus *Paniculata*:—C. *L. bainesii* (*Goldblatt & Manning 8808*).—D. *L. coerulea* (*Seydel 2609*).—E. *L. micrantha* (Klatt) Baker (*Williams 875*). (Variously magnified.)

sia, we conclude that tunics composed of compacted fibers are the primitive condition. Similar, though not identical, tunics occur in *Thereianthus* and *Micranthus*, corms of which can often only be distinguished from those of *Lapeirousia* by being rounded (vs. flat) at the base. Woody tunics are unknown in other genera of Watsonieae, but are present in a few genera of Ixieae (notably *Hesperantha*, *Geissorhiza*, and *Romulea*) where they are most likely also a derived condition.

LEAF ANATOMY (Table 1)

Like all Iridaceae, the leaves of *Lapeirousia* are ensiform and equitant, and consist of a sheathing base and a blade that is typically lanceolate to linear and either plane or occasionally terete (subg. *Paniculata*), or ridged to corrugate (subg. *Lapeirousia*). In transverse section the blades are isobilateral and monofacial, oblong to linear, and variously plane-sided, ridged or zigzag. The marginal subepidermal cells are unlignified apart from the phloem cap that is present in most species, the basic condition for Watsonieae and presumably for the whole family. The intercostal epidermal cells are brick-shaped and thin-walled, although the outer periclinal walls may sometimes be slightly thickened. There is a notable correlation between leaf anatomy and subgeneric limits in the structure of the costal epidermis (Table 1). In subg. *Lapeirousia* the costal cells are abruptly enlarged and often heavily thickened in the outer periclinal walls, and the ridge is square and truncate (Fig. 2B). In subg. *Paniculata* the epidermis cells gradually diminish in size and usually lack a heavily thickened outer periclinal wall, and the ridges are smoothly rounded (Fig. 2A).

The vascular bundles are in two rows with larger (major) bundles separated by one or two smaller (minor) bundles; major bundles occupy the ridges and minor ones the intervening troughs. The xylem poles face the center of the leaf. The two subgenera differ somewhat in the arrangement of the bundles. Although the major bundles are, with one exception (Table 1), alternate in subg. *Lapeirousia* (Fig. 2B), they are mostly, but not always, opposite in subg. *Paniculata* (Fig. 2A). This is an obvious determinant of the zigzag leaves in subg. *Lapeirousia* and plane leaves in subg. *Paniculata*. (In species with largely alternate bundles the central bundles are often opposite, but the pairs become more alternate distally.) The zigzag leaf form is a specialization in subg. *Lapeirousia*, and the accompanying alternation of the major bundles is probably so, given that all other genera of Watsonieae have opposed bundles. A pseudomidrib formed by larger central bundles is not evident in subg. *Lapeirousia* even though the central bundle in *L. divaricata* is sufficiently large to form a pseudomidrib. This species resembles subg. *Paniculata* in having opposite bundles, but the ridges are those of subg. *Lapeirousia*, and the corm tunics place it firmly in the latter. The opposed bundles in *L. divaricata*, a fairly specialized species, are presumably secondary. A pseudomidrib is present in all plane-leaved species of subg. *Paniculata*, even those in which the vascular bundles are alternate (*L. coerulea* and *L. avasmontana*), as well as in nearly all species of the tribe, and this is undoubtedly the basic condition. The alternation of bundles in *L. coerulea* and *L. avasmontana*, thought to be the most primitive species in subg. *Paniculata*, is puzzling. On the basis of outgroup comparison, this must be viewed as a specialization for the two species.

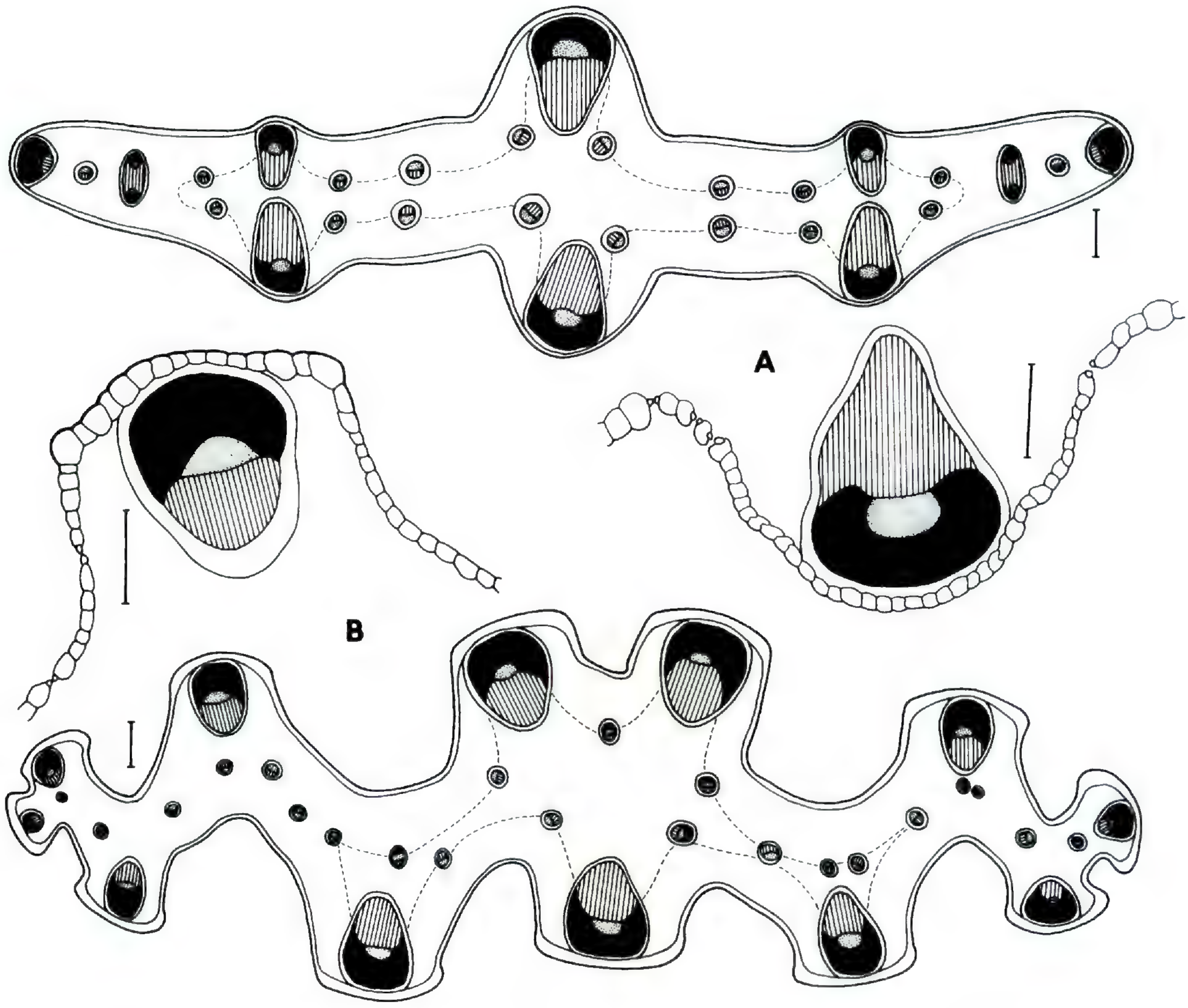

FIGURE 2. Transverse sections of leaf blades and vascular bundles in *Lapeirousia*.—A. Subgenus *Paniculata*: *L. bainesii*.—B. Subgenus *Lapeirousia*: *L. odoratissima*. Scale bars = 150 μm. (Voucher data in Table 2.)

The major bundles reach the epidermis or are separated from it by a single layer of parenchyma, while the minor bundles are a number of cell layers below the epidermis. In species with opposite bundles, some vascular bundles may fuse at the xylem poles. An outer bundle sheath is present as a single layer of parenchymatous cells distinct from the surrounding mesophyll cells. An inner sheath is present as a phloem cap in at least the central major bundles, and usually all major bundles; and the phloem cap may also occur in some minor bundles. (In *L. corymbosa* alone there is a more or less complete sclerenchyma sheath, which is more tenuous at the xylem pole and is restricted to the central bundles.) Even when the phloem cap is absent from some minor bundles, the marginal bundles are still usually capped (but not in *L. anceps*, *L. pyramidalis*, and *L. corymbosa*). Crystals are present, mainly in the outer bundle sheaths but also in isolated mesophyll cells. Chlorenchyma may be distinct from the central ground tissue or may grade into it.

Pillansia, the only genus of Ixioideae–Pillansieae, and the other genera of Watsonieae (*Savannosiphon*, *Micranthus*, *Thereianthus*, and *Watsonia*) each differ from *Lapeirousia* in some aspect of their leaf anatomy (Table 1). *Pillansia* is characterized largely by primitive traits (Goldblatt, 1990a). The leaf is plane in transverse section, and lacks a distinct midrib and ridges, although it is thickened toward the center and the profile is undulate. The epidermal cells are uniformly square without differentiation between costal and intercostal, although stomata are restricted to the intercostae. The vascular bundles are in two opposite rows of alternating major and minor pairs, and all except one or two very minor bundles are subepidermal and reach the epidermis, although the outer sheath is not distinct from the surrounding chlorenchyma at the phloem pole. All bundles have

a sclerenchyma phloem cap. A marginal bundle is absent, and there is no subepidermal marginal sclerenchyma.

In *Savannosiphon* the plane leaf also has all the vascular bundles subepidermal and of similar size. In *Micranthus* most of the bundles are subepidermal with some of the very minor bundles more deeply embedded in the leaf. All major bundles, including the marginal ones, have a complete sclerenchyma sheath well-developed at both poles. *Thereianthus* is likewise characterized by a complete sclerenchyma sheath around the major bundles, at least those in the center of the leaf, but the minor bundles have a phloem cap only and are embedded in the mesophyll. The marginal bundles lack sclerenchyma. We assume that a complete sclerenchyma sheath is a synapomorphy for *Micranthus* and *Thereianthus*. The latter differs further from the other genera in having nonvascularized flanges on the leaf margins, but not all species of the genus have been examined for this character. *Watsonia* resembles most species of *Lapeirousia* subg. *Paniculata* in the distribution and nature of the vascular bundles: two opposed rows of large subepidermal bundles separated by embedded minor bundles with sclerenchyma largely restricted to the phloem cap. It is distinct in the tribe in the extensive development of subepidermal sclerenchyma in a V- or U-shaped region at the leaf margin, associated with and extending well beyond the marginal phloem caps. There is a similar development of sclerenchyma in some genera of Ixioideae, and in Iridoideae–Irideae, e.g., *Dietes* (Rudall, 1983), and the shrubby genera of Nivenioideae (Rudall & Burns, 1989). In the last-mentioned two groups the sclerenchyma is not associated with the marginal bundles. There is little doubt that the presence of subepidermal sclerenchyma on the leaf margins is a specialized condition and a synapomorphy for *Watsonia* in addition to those recognized by Goldblatt (1989).

Discussion

The five genera of Watsonieae comprise a monophyletic line united by the derived deeply divided style branches and the absence of flavone *O*-glycosides (Goldblatt, 1989, 1990a). The sister tribe, Ixieae, differs by having a putatively more specialized type of corm ontogeny and by having flavones and flavone *O*-glycosides. Within Watsonieae, *Watsonia* constitutes one clade and the four remaining genera a second. Several synapomorphies unite the species of *Watsonia* (Goldblatt, 1989), and now the presence of subepidermal marginal sclerenchyma can be added. The clade formed by *Thereianthus*, *Micranthus*, *Lapeirousia*, and *Savannosiphon* share three synapomorphies: small corms; corm tunics formed only from the cataphylls (the foliage leaves are inserted on the flowering stem and do not contribute to the tunics); and corm tunics composed of densely compacted fibers (previously defined as hard or woody by Goldblatt, 1989). Only subg. *Lapeirousia* has truly woody tunics of a uniform texture and smooth surface. *Thereianthus* and *Micranthus* comprise one clade, defined by their fusiform seeds (Goldblatt, 1989). The presence of complete sclerenchymatous bundle sheaths in the leaves is a possible additional synapomorphy (only three of the ten species in the two genera have been examined for this character), although this xeromorphic feature is a fairly common condition in Iridaceae.

Savannosiphon, which is monotypic, and *Lapeirousia* are weakly related (Goldblatt, 1989). They both have angular to winged stems and coriaceous capsules (polarization of the latter character is uncertain). Leaf anatomy makes no contribution to our perception of this clade.

The unusual flat-based corms of *Lapeirousia*, the major synapomorphy for the genus (Goldblatt, 1989), separate it from *Savannosiphon* whose included styles and stamens readily distinguish it from other Watsonieae. The position of the vascular bundles in *Savannosiphon* resembles that in *Pillansia*, but whether this represents a reversal to the primitive state or an indication that the genus is misplaced in our phylogeny (Fig. 3) is uncertain.

Within *Lapeirousia* there appear to be two major groups (Fig. 3) defined by their corm tunics, leaf morphology, and anatomy. Species with woody tunics of uniform texture and a smooth surface, corrugate leaves with truncate ribs, and mostly alternate veins form one clade, which we recognize as subg. *Lapeirousia*. The remaining species are plesiomorphic for these characters (Table 1) but have a presumably derived inflorescence structure (Goldblatt, 1990b), and we recognize the group as subg. *Paniculata*. In general, species of subg. *Paniculata* have highly branched inflorescences (pseudopanicles) (Fig. 4A, B), whereas those of subg. *Lapeirousia* generally have spikes (Fig. 4C), although these may also be branched to some degree. Some members of subg. *Paniculata*, notably *L. abyssinica*, have few-branched inflorescences that are indistinguishable from those of subg. *Lapeirousia*. A simple or few-branched spike is presumed to be the basic condition in Watsonieae and Ixieae (Goldblatt, 1990a, b). Species of subg. *Lapeirousia* have herbaceous bracts that are often

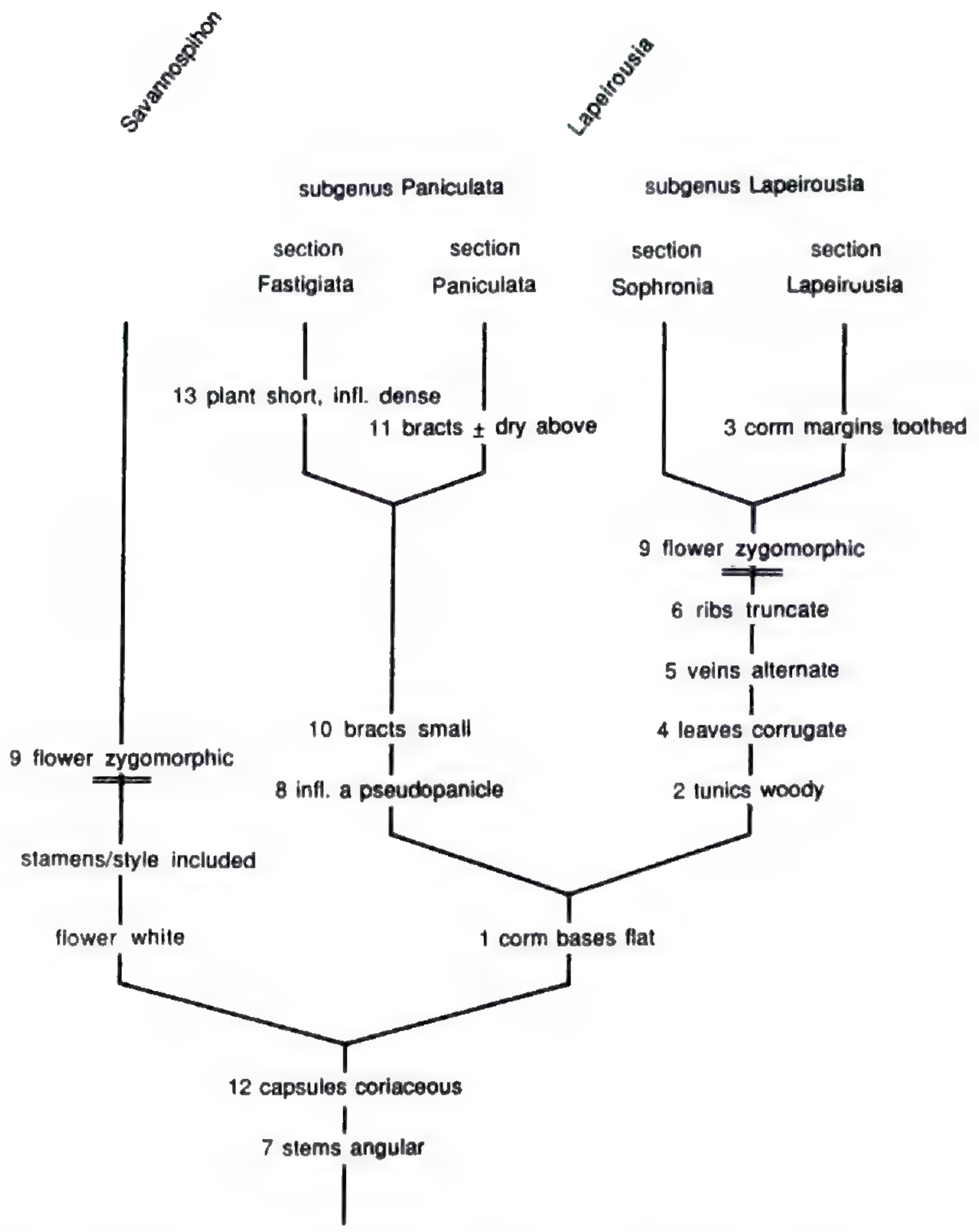

FIGURE 3. Hypothetical phylogeny of *Lapeirousia* showing the major infrageneric lineages and the apomorphic characters that define them. Characters used in the cladogram are listed in Table 3.

enlarged and sometimes ridged, keeled, or toothed. In subg. *Paniculata* the bracts are generally small and either entirely herbaceous or partly membranous and are often dry at anthesis. We assume that small bracts constitute a second, weak, synapomorphy for the subgenus (Table 2), as large, firm herbaceous bracts are the presumed basic condition for the tribe. Thus subg. *Lapeirousia* has diverged in the nature of its vegetative organs whereas subg. *Paniculata* has to some extent in the floral axis.

The occurrence of actinomorphic flowers in three species of subg. *Paniculata*, *L. corymbosa* (from the southwest Cape) and *L. coerulea* and *L. avasmontana* (from Namibia) remains puzzling. These species do not appear to be closely related but they may well be primitive in the subgenus, and there seems no reason to believe that the actinomorphic flower is a derived trait in a genus of largely zygomorphic-flowered species. We accept here that actinomorphy is the primitive condition for the genus and that zygomorphy must have evolved independently in each subgenus of *Lapeirousia* as well as in *Savannosiphon*. There is considerable floral convergence in Ixioideae, and there are single instances of presumably primitive actinomorphy in the otherwise zygomorphic-flowered genera *Watsonia* (Goldblatt, 1989) and *Thereianthus* (Lewis, 1941).

By contrast, in subg. *Lapeirousia* the zygomorphy is thought to be the basic state and actinomorphy derived in the few species in which it occurs (Goldblatt, 1972). These actinomorphic species are all acaulescent, and we assume that actinomorphy is adaptive for these low-growing plants whose flowers are borne close to the ground—vertical presentation with consequent actinomorphy enhances floral display and access to long-tongued pollinators.

A further refinement of the infrageneric classification of *Lapeirousia* is suggested by discontinuous patterns of variation in both subgenera (Fig. 3). All the Cape species of subg. *Paniculata* have dark corm tunics, a trait only occasionally found in the tropical African species; fairly short, falcate leaves; rather congested inflorescences; and usually low stature (Fig. 4D). These species also have a basic chromosome number of $x = 10$ (Goldblatt, 1971, 1972), whereas the tropical species range from $n = 8$ to $n = 3$ (Goldblatt, 1990c). The bracts of the tropical species are characteristically dry at anthesis (there are a few exceptions), which we

FIGURE 4. Representative species of *Lapeirousia* showing the morphology of the inflorescence.—A. *L. bainesii* (sect. *Paniculata*).—B. *L. corymbosa* subsp. *fimbriata* (sect. *Fastigiata*).—C. *L. dolomitica* subsp. *lewisiana* (sect. *Lapeirousia*).—D. *L. odoratissima* (sect. *Sophronia*). Scale: ×0.5.

assume is a derived state (Table 2). We suggest that the tropical and Cape members of subg. *Lapeirousia* constitute two monophyletic lines for which we propose sectional rank: sect. *Fastigiata* for the Cape species and sect. *Paniculata* for the tropical species.

In subg. *Lapeirousia* those species with the specialization of elaborate, toothed to spiny lower corm tunic margins probably constitute a monophyletic line and also merit sectional segregation. Whether the remaining species constitute one or more lines remains to be determined. We find no reason to favor a particular hypothesis here but suggest they be segregated in one section, which incidentally contains, among others, all the acaulescent species (Baker's subg. *Sophronia*).

Systematics

Lapeirousia Pourret, Mem. Acad. Sci. Toulouse 3: 79–82. 1788. TYPE: *Lapeirousia compressa* Pourret (= *L. fabricii* (de la Roche) Ker).

1. Subgenus **Lapeirousia**

Plants with hard, woody corm tunics of uniform texture, the surface smooth and often glossy, decaying irregularly into unequal fragments, rarely becoming fibrous, the basal margins sometimes produced into teeth or spines. *Stem* aerial or entirely subterranean. *Leaves* corrugate (shallowly plicate), without a prominent midrib and all major veins ± equal. *Inflorescence* a simple or branched spike, or the internodes very short and forming a tuft at ground level; *bracts* herbaceous, short to long, the margins and keel sometimes undulate, crisped or toothed, the inner shorter than the outer. *Flowers* actinomorphic (only in acaulescent species) or zygomorphic, short- to long-tubed, the upper tepal usually larger than the others, and the lower three with contrasting markings; stamens symmetrically disposed or unilateral and arcuate.

Section **Lapeirousia**

Plants with woody corm tunics with the basal margins toothed or spiny. *Stem* aerial and usually branched. *Inflorescence* a simple or branched spike. *Flowers* always zygomorphic with the stamens unilateral and arcuate.

Eight species occurring in the southwest Cape, Namaqualand and the Karoo, South Africa, and in southern Namibia.

Section **Sophronia** (Lichst. ex Roemer & Schultes) Goldbl. & Manning, stat. nov. *Lapeirousia* subg. *Sophronia* (Lichst. ex Roemer & Schultes) Baker, Handbk. Irideae 174. 1892. *Sophronia* Lichst. ex Roemer & Schultes, Syst. 1: 482. 1817. TYPE: *Lapeirousia plicata* (Jacq.) Diels.

Plants with woody corm tunics with the bases entire, not produced into teeth or spines. *Stem* aerial and usually branched or not produced above the ground. *Inflorescence* a simple or branched spike, or the internodes very short and forming a tuft at ground level. *Flowers* actinomorphic in the acaulescent species or zygomorphic with the stamens unilateral and arcuate.

Ten species mostly in southern Africa, although *L. odoratissima* widespread across south tropical Africa and Namibia.

2. Subgenus **Paniculata** Goldbl. & Manning, subgenus nov. TYPE: *Lapeirousia erythrantha* (Klatt) Baker.

Plantae cormi tunicis duris, fibrosis compactis compositis, foliis usitate planis costatis, raro teretibus, inflorescentia usitate perramoso et ± paniculato, bracteis brevibus subaequalibus aliquando siccis supra.

Plants with hard, persistent corm tunics composed of densely compacted fibers (sometimes ± woody in texture), decaying into vertical strips or becoming fibrous and cancellate to reticulate. *Leaves* usually plane with the midrib and sometimes other veins raised, or sometimes terete. *Inflorescence* usually highly ramified and ± panicle-like (a pseudopanicle) or sometimes a branched spike, the ultimate branches bearing 1–8 flowers, and those below the terminal flower always sessile; *bracts* short, herbaceous, sometimes dry apically or for their entire length at anthesis, the inner bracts about as long as the outer ones.

Seventeen species occurring in the southwest Cape, South Africa, and in tropical Africa from central Namibia to Ethiopia and Nigeria.

Section **Paniculata**. TYPE: as for the subgenus.

Plants usually very branched. *Corm* tunics pale straw to blackish, decaying into regular vertical strips or becoming fibrous and reticulate. *Leaves* plane or rarely terete, the midvein sometimes raised, usually straight, sometimes weakly falcate. *Inflorescence* a pseudopanicle or rarely a branched spike, usually lax but the flowers sometimes congested at the end of the branches; *bracts* herbaceous to membranous, usually becoming dry in the

upper half by anthesis. *Flowers* actinomorphic or zygomorphic, the tepals subequal or unequal (then with the upper tepal largest and reflexed or arched over the stamens); stamens symmetrically disposed or unilateral and arcuate.

Fourteen species extending from central Namibia, Botswana, and the Transvaal across central Africa to Ethiopia in the north and Nigeria in the west.

Section **Fastigiata** Goldbl., Contrib. Bolus Herb. 4: 15. 1972. TYPE: *Lapeirousia corymbosa* (L.) Ker.

Plants usually very branched. *Corm* tunics dark brown to black, decaying into regular vertical strips. *Leaves* plane, the midvein sometimes raised, falcate or straight. *Inflorescence* a pseudopanicle or a spike, usually congested; *bracts* herbaceous, the apices often reddish or purple. *Flowers* actinomorphic or zygomorphic, the tepals subequal; stamens symmetrically disposed or unilateral and arcuate or declinate.

Three species restricted to the southwest Cape, South Africa.

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CYTOLOGICAL VARIABILITY IN THE AFRICAN GENUS *LAPEIROUSIA* (IRIDACEAE–IXIOIDEAE)[1]

Peter Goldblatt[2]

ABSTRACT

The African genus *Lapeirousia* (Iridaceae–Ixioideae) comprises two subgenera each with two sections. The basic chromosome number for the genus is postulated to be $x = 10$ in a strongly bimodal karyotype with one long and nine much smaller pairs. This karyotype occurs in at least some species of three sections and is exclusive in subg. *Paniculata* Goldbl. & Manning sect. *Fastigiata* Goldbl. In subg. *Lapeirousia* the bimodality is preserved in all species, but chromosome number ranges from $n = 10$ to 8. Genera most closely allied to *Lapeirousia* also have $x = 10$ and asymmetric but less strongly bimodal karyotypes. Sect. *Paniculata*, which is entirely tropical in distribution, has species with $n = 8, 7, 6, 5, 4$, and 3. Species of the section with the highest chromosome numbers have bimodal karyotypes with one longer chromosome pair. Total chromosome length, a crude measure of genome size, is similar in all except two species, which have $n = 6$ and approximately twice the total chromosome length compared with all other species examined. Polyploidy appears to have been involved in the evolution of only these two species. Dysploid reduction is thought to have been responsible for the variation in chromosome number noted in other species. Evidence from comparative morphology suggests that descending dysploidy occurred repeatedly in the genus and that low numbers, $n = 4$ and 3, were achieved in separate lineages.

Lapeirousia Pourret, a genus of Iridaceae–Ixioideae (cf. Goldblatt, 1990a), comprises some 35 species (Goldblatt, 1972, 1990b; Goldblatt & Manning, 1990) distributed in two subgenera each with two sections. The genus is widespread in Africa south of the Sahara, with centers in the winter-rainfall zone of the southern African west coast and in the drier parts of tropical Africa, particularly Namibia. This pattern is unusual for Iridaceae, in which most African genera are either restricted to the Cape region of South Africa or extend into the wetter parts of eastern southern Africa, some as far north as Ethiopia. Only *Gladiolus* (Ixioideae), *Moraea* (Iridoideae), and *Aristea* (Nivenioideae) have ranges comparable to *Lapeirousia*, but they are absent or poorly represented in areas of tropical Africa where *Lapeirousia* is best developed (Goldblatt, 1990b).

Chromosome cytology of *Lapeirousia* in southern Africa in moderately well documented, with nine species counted, about half the total (Goldblatt, 1971, 1972), but until now there have been no counts for any tropical African species. The karyotypes of 13 species in tropical Africa (of a total of 16) and an additional seven in southern Africa are described here. The cytology of only five species remains unknown. Data indicate that *Lapeirousia* is unusually variable cytologically. Haploid numbers of $n = 10, 9, 8, 7, 6, 5, 4$, and 3 have now been recorded in the genus. This contrasts with the majority of Ixioideae, which are cytologically uniform (Goldblatt, 1971) and typically have only one base number and relatively little polyploidy. Only *Romulea* and *Crocus* have until now been exceptions to this pattern in the subfamily (De Vos, 1972; Brighton, 1976a, b, 1977).

Variation in chromosome number in *Lapeirousia* is accompanied by major differences in karyotype. Strong bimodality appears to be the rule (Goldblatt, 1972), with one long chromosome pair and a variable number of much smaller pairs (Goldblatt, 1971, 1972). The bimodality encountered in all southern African species examined also occurs in some of the tropical species. The patterns

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of variation in form and overall size of the chromosome complements in *Lapeirousia* and in closely allied genera suggest that the direction of chromosome change has been from high to low numbers and that polyploidy has played only a minor role in the evolution of the genus.

Materials and Methods

Wild-collected seeds or corms (Table 1) were sprouted in the greenhouse. Root tips, harvested when 1–2 cm long, were pretreated either in 0.003 M hydroxyquinoline for 6–8 hours at refrigerator temperature or in saturated aqueous 1-bromonaphthalene at room temperature for 3 hours, and then fixed in 3 : 1 absolute ethanol–glacial acetic acid for 1–2 minutes. Tips were then stored in 70% ethanol or immediately macerated in 10% HCl at 60°C for 6 minutes, washed in tap water, and later squashed in lactopropionic orcein (Dyer, 1963) or FLP orcein (Jackson, 1972). This method differs from the paraffin-section technique I previously used for *Lapeirousia* (Goldblatt, 1971, 1972) and has yielded more satisfactory results. Difficulties, noted previously, in growing corms were still encountered and an adequate number of root tips for study could be obtained only with difficulty in several species. Seeds, however, germinate easily and provide ample material for examination.

Total length of the chromosome complement was determined in selected species (Table 2) by linear measurement of camera-lucida-drawn chromosomes in karyotypes of estimated comparable degree of contraction and figured at the same magnification. Error in this type of estimation of genome size is considerable, but the results appear internally consistent so that some confidence can be attached to the results.

Observations

Subgenus *Paniculata* section *Paniculata*

Restricted to tropical Africa and previously uncounted, sect. *Paniculata* is remarkably variable cytologically. The two putatively most primitive members of the section and the only ones with actinomorphic flowers, *L. avasmontana* and *L. coerulea*, have $2n = 16$ and 8, respectively. The karyotype of *L. avasmontana* (Fig. 1A) consists of one long acrocentric chromosome pair ca. 8 μm long and seven short acrocentric to submetacentric pairs ca. 3 μm long. No satellites were noted.

Lapeirousia coerulea, for which there are counts for seven populations, has a very different karyotype (Fig. 1B). In all populations there are two pairs of longer acrocentric pairs 5–6 μm long (up to 7 μm in some preparations where the chromosomes are less contracted), and two pairs of acrocentric to submetacentric chromosomes 2.3–3 μm long. When satellites are visible (three of the seven populations examined) they are small and situated on the end of a short arm of one of the small chromosome pairs. In one population, *Lavranos & Pehlemann 21101* (Table 1), small constrictions are present near the ends of the long arms of a long chromosome pair, and no satellites were noted in these plants.

The widespread *Lapeirousia erythrantha* has $2n = 12$ in all eight populations examined, these covering a substantial part of the range of the species from southern Malawi to northern Zambia. The karyotypes are similar in all plants examined, with the exception of those with B chromosomes, and consist of three longer acrocentric pairs 6–7 μm long and three shorter acrocentric pairs 3.3–4 μm long (Fig. 1C). Size differences are not as sharp as in the preceeding two species. Small satellites are present on the ends of the short arms of one of the longer pairs. One to three B chromosomes were noted in plants from Mufulira, Zambia (*Goldblatt 7575*). The B chromosomes varied in number in different plants and are identified by their particularly small size, ca. 1 μm smaller than the next smallest chromosomes. A collection from eastern Zambia (*Faden et al. 74/83*), which has $2n = 14$, is probably best interpreted as having $2n = 12 + 2B$. There are four small pairs in this collection and the smallest of these are probably B chromosomes.

Lapeirousia rivularis, evidently closely related to *L. erythrantha*, also has $2n = 12$ (Fig. 1D), although one seedling examined had $2n = 18$ and is apparently triploid. The karyotype of the $2n = 12$ plants closely resembles that of *L. erythrantha*. Total chromosome length in these two species (Table 2) is close to twice that of all the other species studied, suggesting their possible polyploid origin.

Two species apparently closely related to *Lapeirousia erythrantha*, *L. abyssinica* and *L. setifolia*, have $2n = 8$. They have similar karyotypes with two long acrocentric pairs 5.5–6.5 μm long (to 9 μm in preparations of less contracted chromosomes) and two much shorter pairs ca. 3 μm long. Small satellites are located on the end of the long arm of a long pair in *L. abyssinica* (Fig. 1E) and on the end of the short arm of a long pair in *L. setifolia* (Fig. 1F). In the latter, one of the small chromosome pairs is metacentric. Total chromosome length in *L. abyssinica* and *L. setifolia* (Table 2) is similar and about two-thirds that of *L. ery-*

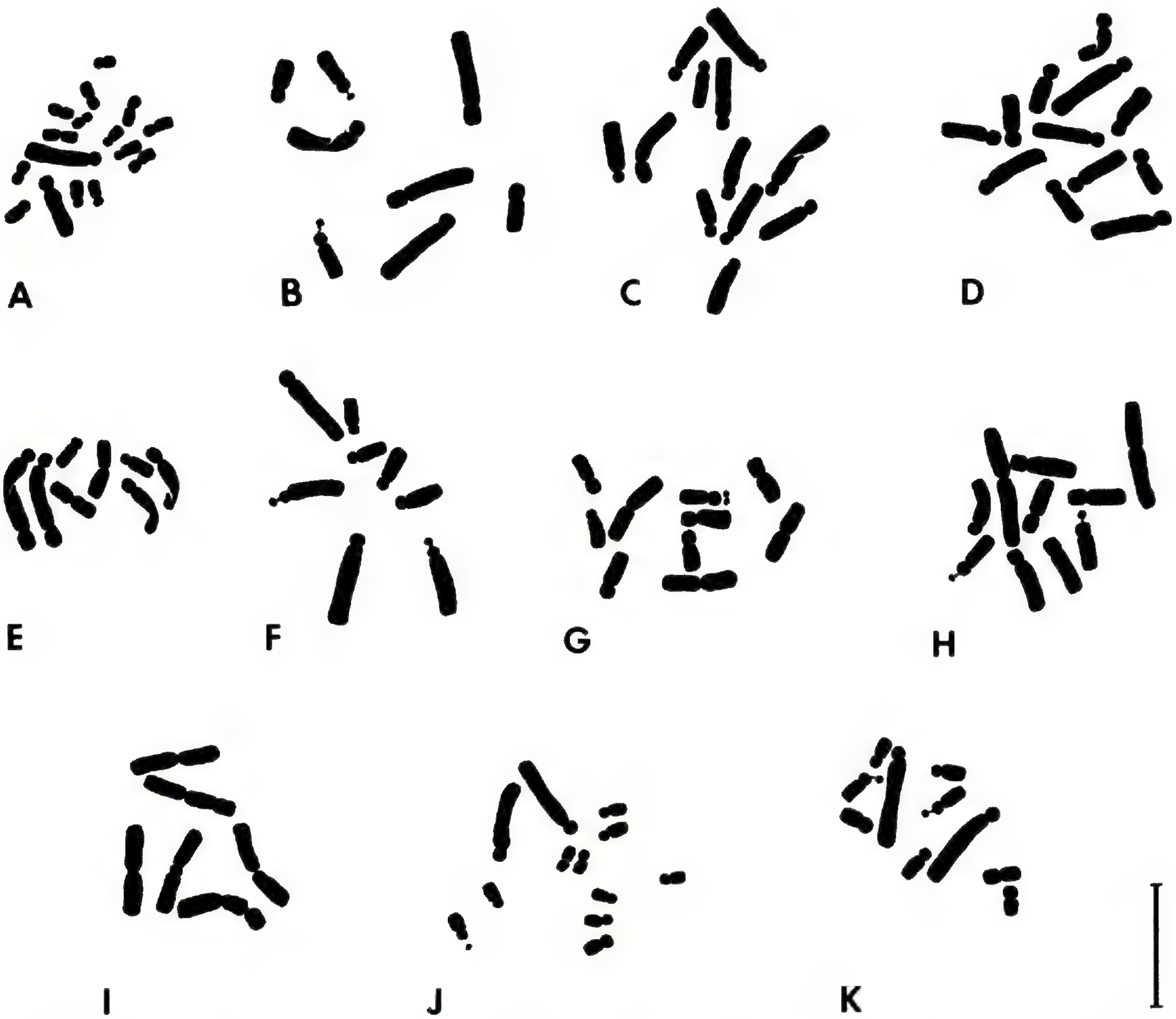

FIGURE 1. Mitotic metaphase in *Lapeirousia* subg. *Paniculata* sect. *Paniculata*.—A. *L. avasmontana*.—B. *L. coerulea*.—C. *L. erythrantha*.—D. *L. rivularis*.—E. *L. abyssinica*.—F. *L. setifolia*.—G. *L. otaviensis*.—H. *L. schimperi*.—I. *L. bainesii*.—J. *L. gracilis*.—K. *L. sandersonii*. Vouchers are given in Table 1. Scale bar, 10 μm.

thrantha (and *L. rivularis*). Other species closely allied to *L. erythrantha* are unknown cytologically, and there are no counts for *L. erythrantha* from Mozambique, Zimbabwe, or Zaire. Counts for this species, however, include both major variants, the small- and crimson-flowered typical form from the southeast part of its range and the blue-flowered form (corresponding to the type of *L. briartii*) from northern Zambia. The lack of any obvious structural variation among the populations examined is notable in view of the morphological variability and wide distribution of *L. erythrantha*.

Three of the six long-tubed species of sect. *Paniculata*, *Lapeirousia otaviensis*, *L. bainesii*, and *L. schimperi*, have similar basic karyotypes with $2n = 10$. Their karyotypes consist of one pair of long submetacentric (almost metacentric) chromosomes 8–10 μm long (depending on the degree of contraction), and four shorter pairs 3.5–6 μm long that show no sharp size discontinuities (Fig. 1G, H). The longest of the latter four pairs is nearly metacentric, and the others are acrocentric. Satellites are present on the ends of the short arms of one of the shorter acrocentric pairs in *L. otaviensis* and *L. schimperi*. Satellites were not seen in populations of *L. bainesii* with this karyotype. Two populations of *L. bainesii* (Table 1) have $2n = 6$ (Fig. 1I) and nearly equal metacentric chromosome pairs 7.5–8 μm long. There are secondary constrictions close to the centromere in one pair and in the midpart of an arm on another.

Two other long-tubed species, *Lapeirousia gracilis* and *L. sandersonii*, have $2n = 12$ and 10, respectively, but otherwise identical bimodal karyotypes with one long acrocentric pair ca. 8 μm long and either five or four much shorter acro-

TABLE 1. Chromosome numbers in *Lapeirousia*. Original counts are marked with an asterisk. The taxonomy used here is based on the revisions of Goldblatt (1972, 1990b). Previous counts were reported by Goldblatt (1971, 1972). Acronyms (abbreviated according to Holmgren et al., 1981) following the collection data refer to the herbaria in which the vouchers are housed. Presence of a bimodal karyotype indicated by Y, absence by N.

Species	Diploid number	Karyotype	Collection data
Subgenus *Paniculata*			
Section *Paniculata*			
L. abyssinica (A. Rich.) Baker	8*	N	Ethiopia, Muger valley, *Edwards et al. 97* (MO)
L. avasmontana Dinter	16*	Y	Namibia, near Windhoek, *Goldblatt & Manning 8798* (MO)
L. bainesii Baker	10*	N	Namibia, ENE of Otjiwarongo, *Lavranos & Pehlemann 21031* (MO)
	6*	N	Namibia, farm Norabis, *Goldblatt & Manning 8826* (MO); Steinhausen road E of Windhoek, *Goldblatt & Manning 8808* (MO)
L. coerulea Schinz	8*	N	Namibia, Ameib, *Giess 15284* (WIND); Ameib, *Goldblatt & Manning 8811A* (MO); Grootfontein, Valhal, *Goldblatt & Manning* no voucher; NW of Omaruru, *Wanntorp 805* (S); Etosha Pan, *Giess 15283* (MO); N of Tsumeb, *Lavranos & Pehlemann 21101* (WIND); W of Otavi, J. *Lavranos & I. Pehlemann* no voucher
L. erythrantha (Klotzsch ex Klatt) Baker	12*	N	Malawi, University of Malawi, Zomba, *Goldblatt 7521* (MO); Thondwe W of Zomba, *Goldblatt 7575* (MO); Old Naisi Road, Zomba, *Goldblatt 7514* (MO); near Ncheu, *Goldblatt 7534* (MO); near Chileka, *Goldblatt 7524* (MO); Chongoni Forest, *La Croix 2698* (MO); Zambia, Chati Reserve, *Goldblatt 7567* (MO); Mufulira, *Goldblatt 7575* (MO).
	14(? = 12 + 2B)		Zambia, Sanje Hill, *Faden et al. 74/83* (MO)
L. gracilis Vaupel	12*	Y	Namibia, Asab, *Goldblatt & Manning 8870* (MO)
L. otaviensis R. Foster	10*	N	Namibia, Auros farm, *Goldblatt & Manning 8837* (MO)
L. rivularis Wanntorp	12, 18*	N	Zambia, Lusaka, *Goldblatt 7537* (MO)
L. sandersonii Baker	10*	N	South Africa, Transvaal, E of Pretoria, Anon sub *Goldblatt 5490* (MO)
L. schimperi (Asch. & Klatt) Baker	10*	N	Namibia, farm Vaalwater, *Goldblatt & Manning 8831* (MO); Zambia, Mufulira, cultivated Missouri Botanical Garden, *Goldblatt s.n.* (MO); Zimbabwe, Victoria Falls, *G. McNeil* no voucher; Malawi, Nyika, *I. La Croix* no voucher
L. setifolia Harms	8*	N	Malawi, Nyika Plateau, *La Croix 4321* (MO); Nyika, *Pawek 6674* (MO)
Section *Fastigiata*			
L. corymbosa (L.) Ker			
subsp. *corymbosa*	20	Y	Goldblatt (1971, 1972)
subsp. *fastigiata* (Lam.) Goldbl.	20	Y	Goldblatt (1971)
L. falcata	20	Y	Goldblatt (1972)
L. micrantha (Klatt) Baker	20	Y	Goldblatt (1971, 1972)
	20*	Y	South Africa, Cape, Cedarberg, near Algeria, *Goldblatt 5150* (MO)
Subgenus *Lapeirousia*			
Section *Sophronia*			
L. anceps (L.f.) Ker	20	Y	Goldblatt (1971)
	20*	Y	South Africa, Cape, S of Piekeniers Kloof, *Goldblatt 3026* (MO); Koeberg, *Goldblatt 5105* (MO)
L. exilis Goldbl.	18*	Y	South Africa, Cape, N of Springbok, *Goldblatt 2649* (MO)

TABLE 1. Continued.

Species	Diploid number	Karyo-type	Collection data
L. jacquinii N.E. Br.	ca. 20	Y	Goldblatt (1971)
	18*	Y	South Africa, Cape, near Trawal, *Goldblatt* (no voucher)
	18(–20)*	Y	South Africa, Cape, near Klawer, *Goldblatt 2266* (MO)
L. littoralis Baker			
subsp. *littoralis*	16*	Y	South Africa, Cape, E of Springbok, *Wisura s.n.* (NBG)
subsp. *caudata* (Schinz) Goldbl.	16*	Y	Mozambique, near Maputo, *Goldblatt 6585* (MO)
L. odoratissima Baker	16*	Y	Namibia, Gobabis district, *Tölken s.n.* (BOL); ENE of Otjiwarongo, *Lavranos & Pehlemann 21059* (WIND); E of Windhoek, *Goldblatt & Manning 8803* (MO)
	18*	Y	Namibia, Palmfläche, *Merxmuller & Giess 30147* (M); Malawi, *Pawek 8166* (MO)
L. oreogena Goldbl.	ca. 18; 16–18	Y	(Goldblatt, 1971, 1972)
L. plicata (Jacq.) Diels			
subsp. *plicata*	16*	Y	South Africa, Cape, Matjesfontein, *Goldblatt 6091* (MO)
L. pyramidalis (Lam.) Goldbl.	ca. 18	Y	(Goldblatt, 1971)
	20*	Y	South Africa, Cape, foot of Gifberg, *Goldblatt 2196* (MO)
L. silenoides (Jacq.) Ker	20*	Y	South Africa, near Garies, *Goldblatt 2767* (MO)
L. verecunda Goldbl.	18*	Y	South Africa, Cape, Spektakel Pass, *Goldblatt 5710* (MO)
Section *Lapeirousia*			
L. arenicola Schltr.	16*	Y	South Africa, Cape, near Hondeklipbaai, *Goldblatt 4242* (BOL)
L. divaricata N.E. Br.			
subsp. *divaricata*	ca. 20	Y	(Goldblatt, 1972)
	20*	Y	South Africa, Cape, origin unknown, cultivated Missouri Botanical Garden, *Goldblatt s.n.* (MO)
subsp. *grandiflora* Goldbl.	16*	Y	South Africa, Cape, Richtersveld, *Goldblatt 5716* (MO)
L. dolomitica Dinter			
subsp. *dolomitica*	16–18	Y	(Goldblatt, 1972)
	16*	Y	South Africa, Cape, Richtersveld, *G. Delpierre 380* (no voucher); *Williamson 3606* (NBG)
subsp. *lewisiana* (B. Nord.) Goldbl.	16*	Y	South Africa, Cape, near Komkans, *Nordenstam & Lundgren 1715* (S); Kamiesberg, *Goldblatt 3980* (MO)
L. fabricii (de la Roche) Ker	16 + 1B*	Y	South Africa, Cape, near Alpha, *Goldblatt* no voucher
L. violacea Goldbl.	16*	Y	South Africa, Cape, Botterkloof, *Goldblatt* no voucher

Uncounted species: *L. angolensis* Goldbl.; *L. barklyi* Baker; *L. masukuensis* Vaupel; *L. montana* Klatt; *L. teretifolia* (Geerinck et al.) Goldbl.

to metacentric pairs 2.5–3 μm long (Fig. 1J, K). In both species satellites are located on the end of a short arm of a short acrocentric chromosome pair. Total chromosome length in these two species is similar (Table 2) and in the same range as that for most species of *Lapeirousia*, including those with low numbers such as $2n = 4$ and 3.

SUBGENUS *PANICULATA* SECTION *FASTIGIATA*

The bimodal karyotype (Goldblatt, 1971, 1972) already described for sect. *Fastigiata* is confirmed. *Lapeirousia micrantha* (Fig. 2A), counted here from a third population, has $2n = 20$ and a karyotype matching that already described for this and the two other species of sect. *Fastigiata*. There are one long acrocentric pair ca. 8 μm long and nine short acro- to metacentric pairs 2–2.5 μm long. Satellites, when observed, are always located on the short arm of a short acrocentric chromosome pair.

SUBGENUS *LAPEIROUSIA*

Sections *Lapeirousia* and *Sophronia*, including the two tropical African species of the latter, have similar karyotypes (Fig. 2B–H), closely resembling the karyotype described above for *L. micrantha*

TABLE 2. Total length of the chromosome complement in selected *Lapeirousia* species. Measurements were made from illustrations of karyotypes of estimated comparable degree of contraction, drawn at the same magnification. Species are grouped in subgenus and section by chromosome number to facilitate comparison.

Species	Diploid number	Total chromosome length (μm)
Subgenus *Paniculata*		
Section *Paniculata*		
L. avasmontana	16	40.0
L. erythrantha	12	57.3
L. rivularis	12	59.5
L. gracilis	12	34.1
L. otaviensis	10	46.8
L. sandersonii	10	38.2
L. schimperi	10	49.1
L. abyssinica	8	40.5
L. coerulea	8	40.7
L. setifolia	8	38.2
L. bainesii	6	45.5
Section *Fastigiata*		
L. micrantha	20	41.2
Subgenus *Lapeirousia*		
Section *Sophronia*		
L. littoralis		
subsp. *littoralis*	16	43.6
subsp. *caudata*	16	40.6
L. odoratissima	16	39.5
L. anceps	20	43.5
Section *Lapeirousia*		
L. arenicola	16	38.8
L. dolomitica	16	34.1

except for variation in the number of small chromosome pairs (Table 1).

In sect. *Sophronia* there are new counts for nine species, six of which are the first records for these species. Numbers range from $2n = 16$ to 20. *Lapeirousia littoralis* subsp. *littoralis* (Fig. 2B) and the tropical African *L. littoralis* subsp. *caudata* have $2n = 16$. The same number is also found in two acaulescent species, the southern African *L. plicata* subsp. *plicata*, and in two populations of the tropical African *L. odoratissima* (Fig. 2C). A third has $2n = 18$. It is also likely that $2n = 16$ is the correct number for *L. oreogena*, previously reported as ca. 18 and 16–18 (Goldblatt, 1972), an acaulescent species closely related to *L. plicata*. I have been unable to obtain sufficient root tip material of this species to confirm its chromosome number.

In the caulescent members of the section, $2n = 20$ is confirmed for *Lapeirousia anceps* (Fig. 2D) and *L. pyramidalis* (Fig. 2E) and reported for the first time in *L. silenoides*. A diploid number of $2n = 18$ was found in *L. exilis* and in two separate populations of *L. jacquinii*, previously reported as $2n =$ ca. 20.

Counts here for sect. *Lapeirousia* include the first records for three species and additional counts for three more, leaving only one species uncounted. A diploid number of $2n = 16$ is the most common and the only one recorded for *L. arenicola*; *L. divaricata* subsp. *grandiflora*; both subspecies of *L. dolomitica* (Fig. 2F, G), previously reported as $2n = 16–18$ (Goldblatt, 1972); and *L. violacea* (Fig. 2H). The single count for *L. fabricii* is $2n = 16 + 1B$. Only *L. divaricata* subsp. *divaricata* differs in the section with two counts of $2n = 20$. It is possible that $2n = 16$ is basic for sect. *Lapeirousia* and *L. divaricata* and that the additional two pairs in subsp. *divaricata* represent B chromosomes.

DISCUSSION

The extensive variation in chromosome number and karyotype in *Lapeirousia* is puzzling. The patterns of variation are particularly difficult to assess in the tropical sect. *Paniculata*, which is so chromosomally diverse yet appears to comprise a monophyletic assemblage (Goldblatt & Manning, 1990). There is no reason to doubt that the only two actinomorphic-flowered species of the section are similar to the ancestral type of the section. Yet at the chromosomal level these two species, *L. avasmontana* and *L. coerulea*, differ surprisingly. The former has a bimodal karyotype with $2n = 16$, and the latter has $2n = 8$ and weak bimodality. No direct polyploid relationship appears to link them and polyploidy seems an unlikely explanation for the numerical difference. Cells of *L. avasmontana* have about the same amount of chromosome material as *L. coerulea*, based on measurement of total chromosome length (Table 2). More likely, *L. coerulea* is dysploid and its lower chromosome number is the result of chromosome fusion by unequal translocation and loss of centromeres and other nonessential genetic material (Jones, 1974, 1977; Goldblatt, 1979).

I suggest that the basic karyotype in *Lapeirousia* is the strongly bimodal type that occurs in all sections, and exclusively in all but sect. *Paniculata*. Basic number may be $x = 10$, 9, or 8, most likely 10. Base numbers in other genera in Watsonieae (Goldblatt, 1971, 1989; Goldblatt & Ma-

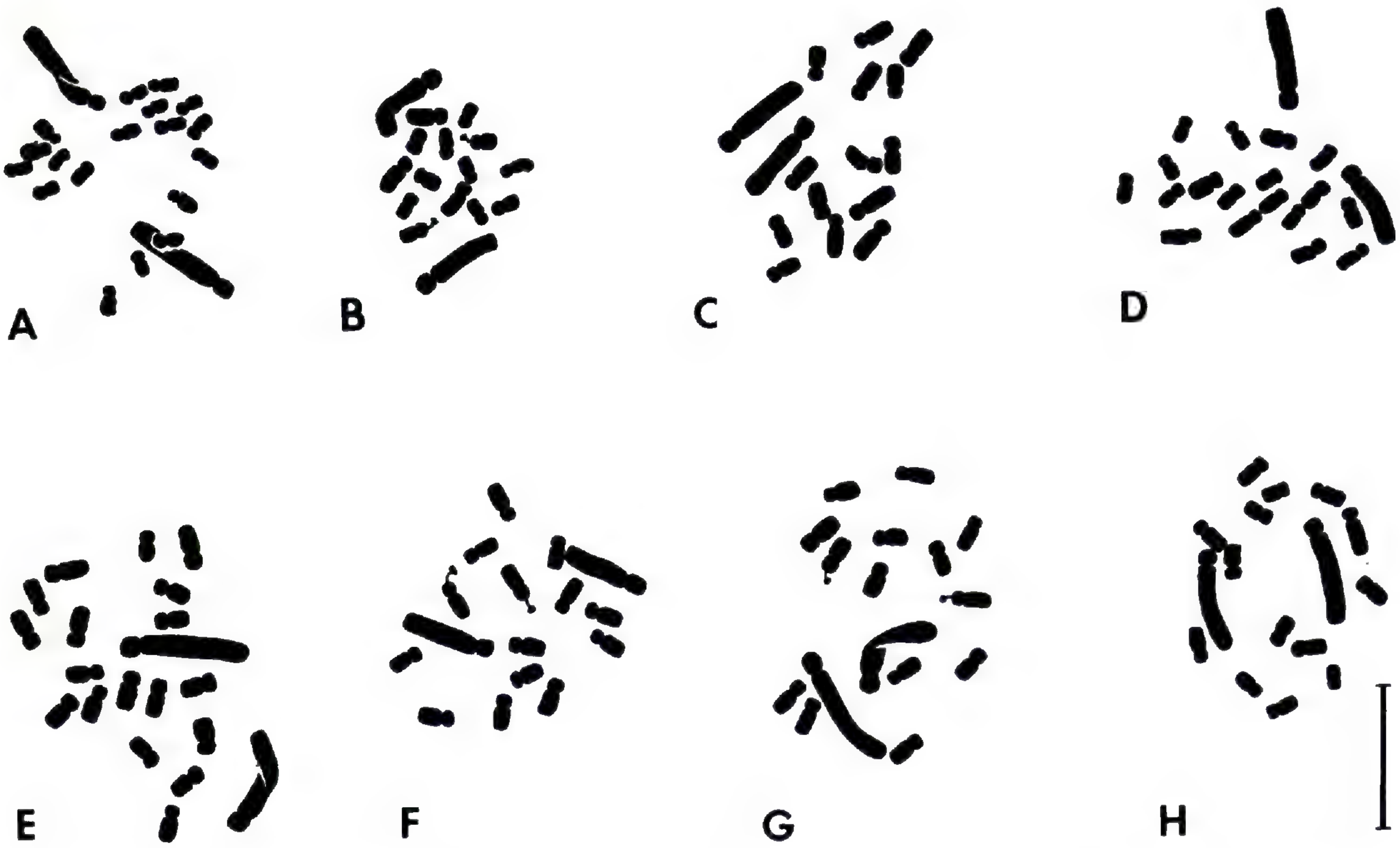

FIGURE 2. Mitotic metaphase in *Lapeirousia* subg. *Paniculata* sect. *Fastigiata* (A) and in subg. *Lapeirousia* sect. *Sophronia* (B–D) and sect. *Lapeirousia* (F–H).—A. *L. micrantha.*—B. *L. littoralis* subsp. *littoralis.*—C. *L. odoratissima.*—D. *L. anceps.*—E. *L. pyramidalis.*—F. *L. dolomitica* subsp. *dolomitica.*—G. *L. dolomitica* subsp. *lewisiana.*—H. *L. violacea.* Vouchers as given in Table 1. Scale bar, 10 μm.

rais, 1976) are $x = 10$ (*Thereianthus* and *Micranthus*), $x = 9$ (*Watsonia*), and $x = 8$ (*Savannosiphon*). The two first mentioned have a bimodal karyotype with one long and nine shorter pairs, and *Watsonia* has two long and seven shorter pairs (Goldblatt, 1971). In all three genera the degree of bimodality is less pronounced than in *Lapeirousia*. *Savannosiphon* (Goldblatt & Marais, 1976) does not have a bimodal karyotype. It seems reasonable to suggest that the ancestral base number and karyotype of *Lapeirousia* were similar to those in *Thereianthus* and *Micranthus*, which probably have the basic karyotype for Watsonieae. The karyotype in *Watsonia* is also probably derived from the *Thereianthus* type (Goldblatt, 1971, 1989).

Structural change appears to have proceeded in both subgenera of *Lapeirousia* toward reduction in number by fusion. The situation in subg. *Lapeirousia* is somewhat confused by the occurrence of two numbers in some species, and this may be the result of the presence of B chromosomes or other types of supernumeraries, which are not uncommon in strongly bimodal karyotypes.

The karyotype appears to be particularly unstable in sect. *Paniculata*. Rapid structural change and accompanying decrease in chromosome number, such as postulated above in *Lapeirousia avasmontana* and *L. coerulea*, appears to be frequent. It is presumed to have occurred within *L. bainesii*, in which $x = 5$ is probably basic. This base number and a similar karyotype are shared with the allied *L. otaviensis* and *L. schimperi*. The low $n = 3$ in two populations of *L. bainesii* can best be explained by so-called Robertsonian fusion of small acrocentric chromosomes to form correspondingly larger metacentrics. Significantly, the measures of total chromosome length (Table 2) are similar in the dysploid *L. bainesii*, and in *L. otaviensis* and *L. schimperi*, which have the presumed basic karyotype for *L. bainesii*.

Strongly bimodal karyotypes are present in *Lapeirousia gracilis*, $n = 6$, and *L. sandersonii*, $n = 5$, both with long-tubed flowers. At least the former appears on morphological grounds (Goldblatt, 1990b) to be closely related to *L. bainesii* and *L. otaviensis*, and this suggests the possibility that the bimodal karyotype may also be ancestral to the rather different basic karyotype in *L. bainesii*, *L. otaviensis*, and *L. schimperi*. Their distinctive karyotype, with its long submetacentric chromosome pair, is presumably the result of ex-

tensive chromosomal rearrangement and fusion. There seems little doubt that the karyotype shared by these three last-mentioned species is a synapomorphy indicating common ancestry.

In *Lapeirousia rivularis* and the species of the *L. erythrantha* group the basic number is difficult to determine. These two species have $2n = 12$ and a total chromosome length half again as much as in *L. abyssinica* and *L. setifolia*, which have $2n = 8$. It seems reasonable to assume that the higher number, $n = 6$, in *L. rivularis* and *L. erythrantha* is polyploid (either dysploid from ancestors with $2n = 16$ or derived from dysploid ancestors with $2n = 6$) and that $n = 4$ in *L. setifolia* and *L. abyssinica* is basic for the alliance. Possibly, $n = 4$ in the latter two species indicates a common ancestry with the actinomorphic-flowered *L. coerulea*, which also has this number. However, there are significant differences in the karyotypes of *L. setifolia*, *L. abyssinica*, and *L. coerulea* so that if this hypothesis is correct, then their karyotypes have diverged appreciably. This model depends very much on crudely determined estimates of genome size (i.e., total linear measurement of illustrated chromosomes; Table 2), and this requires further investigation. Critical measurement of genome size would be particularly useful in evaluating the relationships of the species of sect. *Paniculata*.

The available data suggest that the unusually low numbers for Iridaceae, $n = 4$ and 3, may have been achieved independently in at least two separate lines in subg. *Paniculata* ($n = 4$ in *L. coerulea*, *L. setifolia*, and *L. abyssinica*; $n = 3$ in a population of *L. bainesii*) and possibly more than twice if the hypothesis that *L. abyssinica* and *L. setifolia* are directly related to *L. coerulea* is not correct. Such parallels in dysploid reduction are also known in Iridaceae in *Moraea*, in which $n = 10$ is basic and $n = 6$ (or 5) has evolved in at least four lines independently (Goldblatt, 1976, 1986, unpublished data) and in three with the loss of all intermediate numbers.

The possession of a bimodal karyotype in *Lapeirousia* may be related to its success in particularly arid habitats, among the most extreme in Iridaceae. The frequency of bimodal karyotypes is highest in plants of arid habitats (C. G. Vosa, pers. comm.), prominent examples being Agavaceae and the succulent Asphodelaceae–Alooideae. Numerical instability in bimodal karyotypes is also known, although the reasons are not. The repeated patterns of more than one number in some species of *Lapeirousia* and in all sections except sect. *Fastigiata* may be another example of this phenomenon. In short, the variation in chromosome number and relative size in *Lapeirousia* are remarkable in Iridaceae and for plants in general and merit further investigation for they may lead to a better understanding of the ways in which dysploidy occurs and its adaptive significance. More counts from new populations and methods such as photometric measurement of genome size and Giemsa banding may be useful in understanding better the cytological evolution in the genus.

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BIOLOGIA FLORAL DE UNA COMUNIDAD ARBUSTIVA TROPICAL EN LA GUAYANA VENEZOLANA[1]

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Resumen

El presente estudio analiza la biología floral de 55 especies de plantas de un arbustal en la Alta Guayana Venezolana. El diámetro y el largo de las flores varían significativamente en relación al tipo de unidad de polinización (flor, inflorescencia, o ambas). El diámetro de las flores varía significativamente de acuerdo al color. La longevidad floral es aproximadamente 12 horas para 35 (63.6%) especies. La orientación de las flores es horizontal en 28 (50.9%) especies, hacia arriba en el 40.0% (N= 22), y hacia abajo en el 9.1% (N = 5). Las flores con anteras de dehiscencia longitudinal (N = 36, 69.2%) están orientadas hacia arriba u horizontalmente. Las flores con anteras poricidas (N = 16, 30.89%) se disponen horizontalmente o colgantes. De 49 especies con polinización biótica la recompensa principal es el néctar (N = 20, 40.8%), aunque el polen es ofrecido en combinación (N = 13, 26.6%). Las flores de dos especies de *Clusia* producen resina (N = 2, 4.1%). La relación largo/diámetro de la flor está positivamente correlacionada con el largo promedio del conjunto de insectos polinizadores (N = 49; $r = 0.53$; $P < 0.001$). Un análisis de agrupamiento en base a los caracteres morfológicos florales permite establecer cinco grupos afines a 37% de similaridad. A 90% de similaridad hay varios pares o grupos de especies que coinciden en su período de floración, los cuales pueden tener especies polinizadoras diferentes o similares. Los resultados del análisis de agrupamiento utilizando las especies de polinizadores como caracteres son de poco valor predictivo para agrupar las especies de plantas de acuerdo a caracteres florales similares.

Abstract

This study investigates the floral biology of 55 plant species from a shrub community in the Venezuelan Guayana Highland. Floral diameter varies significantly with color and type of pollination unit (flower, inflorescence, or both). Corolla length varies significantly with the pollination unit. Flower longevity is about 12 hours for 35 (63.6%) of the plant species. Flowers are oriented horizontally in 50.9% (N = 28) of the species, 40.0% (N = 22) upward, and 9.1% (N = 5) downward. Flowers with longitudinally dehiscent anthers (N = 36, 69.2%) are oriented upward or horizontally, whereas species with poricidal anthers (N = 16, 30.8%) are oriented horizontally or downward. From 49 plant species with biotic pollination, the main reward is nectar (N = 20, 40.8%); however, pollen is given as the secondary reward in 26.6% (N = 13) of the species. Pollen alone is offered in 26.6% (N = 13) of the species. The flowers of two species of *Clusia* produce resin. Flower lengths and diameters are not significantly correlated with lengths of insect pollinators. However, the length/diameter ratio of flowers correlates with average size of insect pollinators (N = 49; $r = 0.53$; $P < 0.001$). Cluster analysis on floral characteristics of 55 plant species showed five artificial groups at 37% similarity. At 90% similarity, there are some pairs or groups of species whose flowering periods overlap. Some pollinators can be shared while in other cases the pollinators differ. Plant groups could not be established when they were clustered using pollinator species as characters.

Una de las preguntas que ha intrigado a los ecológos y evolucionistas, es ¿Cómo en comunidades de plantas se mantiene el flujo genético intraespecífico? El estudio de la biología de polinización de una comunidad puede aportar información a esta pregunta. De este modo, el desfasaje de períodos de floración y fructificación entre especies es considerado como uno de los mecanismos que

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evita la interferencia entre especies que comparten polinizadores y dispersores comunes (Snow, 1965; Mosquin, 1971; Gentry, 1974; Frankie et al., 1983; Stiles, 1975; Mori et al., 1978). La morfología floral también puede incrementar la selectividad de los polinizadores (Macior, 1971; Leppik, 1968, 1977; Orians et al., 1977; Feinsinger, 1978; Harder, 1985). La divergencia en los tipos florales ha sido asociada con el desarrollo sensorial de los polinizadores, particularmente en la capacidad de distinguir y recordar ciertos tipos florales (Leppik, 1968). El tamaño floral y el de los polinizadores han permitido establecer algunas relaciones de interdependencia. La hipótesis de repartición del recurso en función del largo de la flor y el largo de la proboscis del insecto destaca un acoplamiento entre ambas estructuras (Ranta & Vepsäläinen, 1980; Harder, 1985). Sin embargo, la especificidad de los polinizadores ha sido sobrestimado y en casos de plantas con floración simultánea se ha encontrado un comportamiento oportunista (Feinsinger, 1978; Frankie et al., 1983; Kephart, 1983).

Estudios de la biología floral en base a las características morfológicas florales y al comportamiento de las plantas en su ambiente contribuyen a entender la biología de polinización. En este contexto, se han estudiado algunos parámetros como parte activa del proceso de polinización. La organización de la inflorescencia, disposición de las flores, dehiscencia de las anteras, y la textura de las flores son características florales que sumados a los colores, longevidad, y recompensa floral, contribuyen a interpretar la biología de polinización a nivel comunitario. Aunque estudios previos han analizado la dinámica reproductiva de varias comunidades (Percival, 1974; Pojar, 1974; Simpson, 1977; Arroyo et al., 1982; Bawa et al., 1985), las interrelaciones entre los atributos morfológicos florales y los tipos de polinización necesitan mayor número de estudios que permitan establecer las características particulares de las comunidades.

Area de Estudio

Esta investigación fue realizada en el Parque Nacional Canaima, sector Gran Sabana, ubicado al sureste del Estado Bolívar, Venezuela. Dicha área forma parte de la cuenca del Río Caroní. El área de estudio seleccionada está situada aproximadamente a 50 km al oeste del Fuerte Luepa, entre Kavanayen y el campamento del Río Parupa (5°35′N, 61°43′O) a una altitud de 1,350 m. Localmente es llamada en lengua Pemon como "Guamu-pe" (Loma Guamu) y "El Jardín," nombre que alude a la abundancia de flores durante todo el año.

El sustrato edáfico esta formado en su mayor parte por areniscas rosadas, rojas o blancas del grupo Roraima, con algunos afloramientos de rocas ígneas (Schubert, 1984). En el área seleccionada, el sustrato edáfico superficial está formado por arenas blancas que se tornan grises en algunos sitios por la materia órganica en descomposición. A poca profundidad del suelo arenoso destaca un enramado de raíces delgadas y gruesas. Frecuentemente afloran grupos de rocas, de tamaño variable y sueltas entre sí, entre las cuales crecen arbustos y hierbas.

La temperatura media mensual de Kavanayen, situada a unos 15 km al este del área de estudio, presenta poca variabilidad a lo largo del año (máxima 21.4°C y mínima 19.9°C). La precipitación media anual es de 2,428 mm (rango: 1,815–3,400 mm), con una precipitación mayor de 100 mm entre abril y diciembre. Los niveles de evaporación superan la precipitación desde enero a marzo, lo que sugiere un balance hídrico negativo.

El área seleccionada ocupa una extensión de aproximadamente 10 hectáreas con una ligera pendiente de aproximadamente 15 grados. La vegetación es achaparrada, 1.0–1.5 m alto, y solo *Clusia grandiflora* destaca por alcanzar hasta 6 m (Ramirez et al., 1988). Esta vegetación se integra con las sabanas circundantes a través de colonias de *Heliamphora heterodoxa* y *Stegolepis angustata* hacia las partes más bajas de la pendiente o por un notorio esparcimiento de arbustos rodeados por Gramineae y Cyperaceae.

Estudios previos sobre la estructura de la vegetación y diversidad florística permiten considerar al área de estudio como un arbustal siempreverde mesotérmico (Huber, 1986), desarrollado sobre suelos arenosos y con un régimen hídrico abundante durante casi todo el año. Ramirez et al. (1988) destacaron un bajo número de especies de plantas vasculares (91), dominado por Melastomataceae (11.8%), Orchidaceae (10.5%), Compositae (7.9%), y Cyperaceae (6.6%). Los períodos de floración y fructificación son mayores de un mes en la mayoría de las especies (Ramirez et al., 1988).

Metodos

Para un total de 55 especies de plantas se realizó un análisis morfológico basado en los tipos florales de Leppik (1977), en la secuencia evolutiva floral (haplomórfico, actinomórfico, pleomórfico, estereomórfico, y zigomórfico), y en la habilidad sensorial de sus polinizadores. Los colores de las flores, incluyendo el color principal y adicionales (guías de néctar, brácteas, estambres llamativos) fueron establecidos utilizando el atlas de colores de Küppers

(1979). Posteriormente se establecieron seis categorías de colores: (1) blanco, considerando flores blancas y blancas amarillentas; (2) Rojo–rosado, considerando flores rojas, rosadas, y fucsia; (3) pardo, considerando flores marrones; (4) moradas, considerando flores morado claro e intenso; (5) amarillo; y (6) verde. Las dimensiones fueron registradas para un total de 10 flores por especie. El largo de flores tubulares representa la longitud floral. En el caso de flores no tubulares, el largo floral representa la medida entre el receptáculo y la altura de pétalos o estambres. El diámetro es la medida entre ápices opuestos de los pétalos. En este caso se realizaron dos medidas perpendiculares.

Las unidades de polinización fueron caracterizadas de acuerdo a la organización de la inflorescencia y al comportamiento de los polinizadores. Cuando las inflorescencias forman grupos densos, uniformes, en forma de seudantos y cuyas flores tienen una antesis relativamente sincronizada, entonces la inflorescencia es considerada la unidad de polinización. En este caso los polinizadores visitan muchas flores simultáneamente, sin moverse de una inflorescencia a otra. Este tipo de organización es considerado como "colectivista" (Burtt, 1961). En el caso opuesto, las unidades de polinización son las flores individuales caracterizadas por inflorescencias laxas y/o sincrónicas en la antesis de las flores. Los polinizadores solo vistan una flor por turno; la visita de otra flor implica su vuelo. Una tercera categoría puede ser considerada como casos intermedios, caracterizado por la organización de las flores parcialmente densa, las cuales están dispuestas en un plano horizontal o ligeramente diferente. La antesis es sincrónica o parcialmente sincrónica. En este caso, los visitantes de gran tamaño se desplazan por la inflorescencia polinizando muchas flores y los visitantes de menor tamaño pueden visitar las flores en forma individualista.

La biología floral fue caracterizada en base a: (1) La orientación de las flores en relación al sustrato, destacando flores orientadas verticalmente hacia arriba y hacia abajo. Las flores dispuestas horizontalmente se denotaron más precisamente de acuerdo a la variación angular hacia abajo y hacia arriba con respecto a un plano horizontal. (2) La longevidad floral fue estimada por observaciones directas en el campo para un mínimo de 10 flores por especies. En cada flor marcada en estado de yema se hicieron anotaciones sobre la receptividad estigmática, presencia de polen, y turgencia de los pétalos a intervalos de seis horas durante dos o más días. (3) El néctar y el polen como recompensa a los polinizadores fueron determinados por observaciones en un mínimo de 10 flores por especie, aisladas en bolsas de pelon. Esta información fue completada con información obtenida del análisis de la morfología floral.

Los agentes polinizadores fueron estudiados para un total de 49 especies de plantas con síndromes bióticos y seis especies anemófilas (cuatro Gramineae y dos Cyperaceae). La proporción de especies anemófilas incluidas en el total de 55 especies corresponde aproximadamente a la proporción natural del arbustal (11 de 91). La actividad de los agentes visitantes se midió mediante períodos de observaciones contínuas de 5 a 15 minutos por especie de planta. En algunos casos el período de observación fue prolongado a 30 minutos. La frecuencia de estos períodos de observación fue de cinco veces al día en cada especie. Esta metodología fue repetida durante tres a cinco días consecutivos o alternos en cada período de trabajo de campo (febrero–marzo; junio–julio y septiembre–octubre). Los agentes visitantes fueron capturados y colocados individualmente en bolsas de celofán. Posteriormente fueron medidos en la longitud del cuerpo. Además se determinó el número de cargas de polen (representado por los distintos tipos de granos de polen) y la posición sobre el cuerpo del animal. La designación de polinizador fue establecida de acuerdo al comportamiento observado y corroborado cuando la posición de la carga de polen sobre el cuerpo del animal hacía contacto con el estigma de las flores.

Las variaciones de los tamaños florales relativos al color, simetría, tipo floral de Leppik (1977), y organización de la inflorescencia fueron establecidas utilizando análisis de varianza de una sola vía. Previo a este análisis se realizó la prueba de homogeneidad de varianza de Bartlett (Sokal & Rohlf, 1969). Las especies de plantas fueron agrupadas de acuerdo a las características florales (morfología y biología floral) y en base a las especies de polinizadores y visitantes previamente reportados (Ramirez, 1989) utilizando un análisis de agrupamiento (SAS, 1982). Este procedimiento está basado en el agrupamiento jerárquico de una matriz de datos multivariados donde los caracteres tienen el mismo peso y las especies son agrupadas de acuerdo al promedio de unión. Esta información fue esquematizada en forma de dendrogramas (SAS, 1982).

Resultados

Morfología floral

Las características morfológicas florales muestran gran variación en cuanto a la simetría, tamaño, color, y orientación (Tabla 1). La simetría y el tipo floral (Leppik, 1977) están claramente

TABLA 1. Características morfológicas, recompensa, y orientación floral de 55 especies de plantas del arbustal.

Familias Especies	Unidad de polinización	Tipo floral (simetría)	Color	Longevidad (días)	Recompensa	Orientación floral	Tipo de dehiscencia	Tamaño floral (mm)		Floración observada
								Largo	Diametro	
Apocynaceae										
1 *Galactophora schomburgkiana* Woodson	In	S (R)	r	2	N	H+	Lo	66.0	66.2	I-II-III
2 *Mandevilla benthamii* (A. DC.) K. Sch.	In	S (B)	a	1	N	H−	Lo	27.5	28.1	I-II-III
Aquifoliaceae										
3 *Ilex retusa* Kl. ex Reiss	i	P (R)	bl	1	Po-N	+	Lo	1.3	2.5	II-III
Araceae										
4 *Philodendron ptarianum* Stey. var. *rugosum* Bunt.	C	Z (B)	bl	10–10	P_f	H	Lo	1.6	1.8	I-II-III
Bignoniaceae										
5 *Digomphia laurifolia* Benth.	In	S (B)	r	2	N	H−	Lo	60.0	44.1	III
Bromeliaceae										
6 *Brocchinia acuminata* L. B. Smith	i	S (R)	bl	1	N-Po	+	Lo	4.4	5.0	II
Compositae										
7 *Calea lucidivenia* Gleason et Blake	C	A (R)	a	1	N-Po	+	Lo	5.2	2.3 (22.6)*	I-II-III
8 *Chromolaena* sp	C	S (R)	m	1	N	+	Lo	5.4	1.2 (3.3)*	I-II
9 *Gongylolepis benthamiana* Rob. Schomb. var. *pubescens* Maguire et Wurdack	In	S (R)	bl	1–2	N	+	Lo	19.4	5.8	I-II
10 *Mikania psilostachya* DC.	C	S (R)	bl	1	N	+	Lo	4.0	0.6 (2.3)*	II-III
11 *Vernonia bolivarensis* Badillo	C	S (R)	m	1	N	+	Lo	4.6	0.9 (3.3)*	I-II
Cyperaceae										
12 *Lagenocarpus rigidus* (Nees) Kunth	i	H (I)	v	3–5	—	+	Lo	2.9	0.6	II-III
13 *Rhynchospora exaltata* Kunth	i	H (I)	v	2	—	+	Lo	2.5	0.7	I III
Cyrillaceae										
14 *Cyrilla racemiflora* L.	i	P (R)	bl	1	N-Po	+	Lo	4.0	3.0	I-II-III
Ericaceae										
15 *Befaria glauca* H. & B.	In	S (R)	r	1–2	N	H−	Pr	20.3	12.5	I-II
16 *Notopora schomburgkii* Hook. f.	In	S (R)	bl	1	N	−	Pr	20.0	12.3	III
17 *Vaccinium euryanthum* A. C. Smith	In	S (R)	r	1–2	N	−	Pr	14.3	12.1	I-II-III

TABLA 1. Continuado.

Familias Especies	Unidad de polinización	Tipo floral (simetría)	Color	Longevidad (días)	Recompensa	Orientación floral	Tipo de dehiscencia	Tamaño floral (mm)		Floración observada
								Largo	Diametro	
18 *Vaccinium puberulum* K. ex Meissner var. *subcrenulatum* (Kl. ex Meissn.) Mag., Steyerm. & Luteyn	In	S (R)	bl	1	N-Po	–	Pr	4.6	5.3	I III
Gentianaceae										
19 *Irlbachia nemorosa* (Willd. ex R. et S.) Merr.	In	P (B)	m	1	N-Po	H–	Lo	8.5	16.4	I-II-III
Gramineae										
20 *Echinolaena inflexa* (Poir.) Chase	i	H (I)	v	2–3	—	+	Lo	1.0	0.5	I-II
21 *Panicum nervosum* Lam.	i	H (I)	v	2	—	+	Lo	1.9	0.7	I-II-III
22 *Paspalum stellatum* H. & B.	i	H (I)	v	2	—	+	Lo	2.9	0.8	III
23 *Trachypogon plumosus* (H. & B. ex Willd.) Nees	i	H (I)	v	2–3	—	+	Lo	1.6	0.5	I III
Guttiferae										
24 *Clusia grandiflora* Splitg.	In	P (R)	bl	1–2	Re-Po	H+	Lo	8.3	62.5	II-III
25 *Clusia pusilla* Stey. subsp. *pusilla*	In	P (R)	bl	1–2	Re-Po	H+	Lo	8.0	59.7	I-II-III
26 *Vismia lauriformis* (Lam.) Choisy	In	P (R)	bl	1	Po	H+	Lo	6.7	5.3	I III
Humiriaceae										
27 *Humiria balsamifera* (Aubl.) St. Hil.	i	S (R)	bl	1	N-Po	+	Lo	1.5	10.6	II-III
Loranthaceae										
28 *Phthirusa adunca* (Meyer) Maguire	i	S (R)	bl	1	N-Po	+	Lo	1.5	8.0	I-II-III
Melastomataceae										
29 *Macairea pachyphylla* Benth.	In	P (B)	bl	1–2	Po	H+	Pr	3.4	12.1	III
30 *Macairea parvifolia* Benth.	In	P (B)	m	1	Po	H+	Pr	3.4	20.2	I
31 *Marcetia taxifolia* (St. Hil.) DC.	In	P (B)	m	1	Po	H+	Pr	1.0	16.4	I-II-III
32 *Meriana sclerophylla* (Naud.) Triana	In	P (B)	m	2–3	Po	H+	Pr	8.3	29.3	I-II-III
33 *Miconia ciliata* (Rich.) DC.	In	P (B)	r	1	Po	H+	Pr	2.4	5.7	I
34 *Siphanthera cordifolia* (Benth.) Gleason	In	P (B)	r	1	Po	H+	Pr	2.6	9.9	I-II-III
35 *Tibouchina fraterna* N. E. Brown	In	P (B)	m	1	Po	H+	Pr	1.4	27.0	I-II-III
36 *Tococa nitens* (Benth.) Triana	In	P (B)	r	1	Po	H+	Pr	13.2	12.9	I-II

TABLA 1. Continuado.

Familias Especies	Unidad de polinización	Tipo floral (simetría)	Color	Longevidad (días)	Recompensa	Orientación floral	Tipo de dehiscencia	Tamaño floral (mm)		Floración observada
								Largo	Diametro	
Myrsinaceae										
37 *Cybianthus quelchii* (N. E. Brown) Agostini	i	P (R)	v	1	Po-N	+	Lo	1.8	4.8	II
Ochnaceae										
38 *Poecilandra retusa* Tul.	In	P (R)	a	1	Po-N	H+	Pr	5.8	25.1	I-II-III
39 *Sauvagesia angustifolia* Ule	In	S (R)	bl	1	N-Po	−	Pr	3.8	6.8	I-II-III
Orchidaceae										
40 *Catasetum discolor* (Lindl.) Lindl.	In	Z (B)	pa	2–3	N	H−		20.0	24.1	II-III
41 *Epidendrum ibaguense* HBK subsp. *ibaguense*	In	Z (B)	r	1	N	H−		9.2	8.1	III
42 *Epistephium duckei* Huber	In	Z (B)	m	1	N	H−	Lo	35.5	18.8	I-II-III
43 *Eriopsis biloba* Lindl.	In	Z (B)	pa	2–3	N	H−		11.3	24.8	III
44 *Pogonia stricta* C. Schweinf.	In	Z (B)	r	1	N	H−	Lo	20.0	10.5	II
45 *Sobralia liliastrum* Lindl.	In	Z (B)	bl	1	N	H−	Lo	41.8	29.8	I-II-III
Rapateaceae										
46 *Stegolepis angustata* Gleason	In	P (R)	a	1	Po	H+	Pr	12.6	24.5	I-II
Rubiaceae										
47 *Borreria capitata* (R. & P.) DC. var. *tenella* (HBK) Stey.	i	S (R)	bl	1	N	+	Lo	2.6	4.5	I III
48 *Declieuxia fruticosa* (Willd.) Ktze. var. *fruticosa*	i	S (R)	bl	1	N	+	Lo	2.6	4.5	I-II-III
49 *Pagameopsis garryoides* (Stand.) Stey.	i	S (R)	m	1	N-Po	+	Lo	3.8	4.5	I-II-III
50 *Remijia densiflora* Benth. subsp. *stenopetala* (Stand. & Stey.) Stey.	In	S (R)	bl	1	N	+	Lo	6.2	8.5	I-II-III
51 *Sipanea galioides* Wernh.	In	S (R)	bl	1–2	N	+	Lo	5.4	21.3	I-II-III
Sarraceniaceae										
52 *Heliamphora heterodoxa* Stey.	In	S (R)	a	2	Po	H−	Lo	31.2	36.0	I-II-III

TABLA 1. Continuado.

Familias Especies	Unidad de polinización	Tipo floral (simetría)	Color	Longevidad (días)	Recompensa	Orientación floral	Tipo de dehiscencia	Tamaño floral (mm) Largo	Tamaño floral (mm) Diametro	Floración observada
Theaceae										
53 *Bonnetia sessilis* Benth.	In	S (R)	bl	1–2	Po	H+	Lo	15.6	60.0	I III
54 *Ternstroemia crassifolia* Benth.	In	S (R)	bl	1	N-Po	–	Pr	6.5	10.0	III
Xyridaceae										
55 *Xyris setigera* Olivier	In	Z (I)	a	1	Po	H+	Lo	1.2	12.2	III

[1] = de acuerdo a Leppik (1977)
[2] = tomado Ramirez et al. (1988)
C = colectivista
i = intermedio
In = individualista
A = actinomórfica
S = estereomórfica
H = haplomórfica
P = pleomórfica
Z = zigomórfica
(B) = bilateral
(I) = irregular
(R) = radial
a = amarillo
bl = blanco
m = morado
pa = pardo
r = rosado–rojo
v = verde
Po = polen
N = néctar
H = horizontal
Re = resina
+ = hacia arriba; – = hacia abajo
Pr = poricida
Lo = longitudinal
( )* = diámetro de la inflorescencia
I = febrero–marzo
II = junio–julio
III = septiembre–Octubre

TABLA 2. Resultados de los análisis de varianza del tamaño floral relativo a cuatro caracteres morfológicos.

Dimensión floral	Color	Simetría	Organización de unidad de polinización	Tipo floral (Leppik, 1977)
Largo	$F_{5.49} = 2.14$[1]	$F_{2.52} = 2.45$[1]	$F_{2.52} = 3.17$[2]	$F_{3.51} = 1.77$[1]
Diámetro	$F_{5.49} = 7.80$[3]	$F_{2.52} = 2.91$[1]	$F_{2.52} = 12.07$[3]	$F_{3.51} = 1.49$[1]

[1] No significativo (prueba de homogeneidad de varianza Bartlett $P < 0.001$).
[2] $P < 0.05$ (prueba de homogeneidad de varianza Bartlett $P < 0.001$).
[3] $P < 0.01$ (prueba de homogeneidad de varianza Bartlett $P < 0.001$).

asociados. Las flores radialmente simétricas son predominantemente de color blanco-cremoso (N = 19, 34.5%) y amarillas (N = 4, 7.3%). Las flores con simetría bilateral son principalmente moradas (N = 7, 12.7%) y rojo-rosadas (N = 5, 9.1%), y las flores sin plano simétrico son de color verde (N = 6, 10.9%). Las flores esteromórficas son principalmente blancas-cremosas (N = 13, 23.6%) y moradas (N = 4, 7.3%), y las haplomórficas son verdes (N = 6, 10.9%). Los colores secundarios o adicionales de flores o estructuras accesorias contrastan con otros colores. Las flores blancas de *Bonnetia sessilis* y de las especies de *Clusia* son llamativas por los estambres amarillos; las flores frecuentemente rosadas de las Melastomataceae presentan filamentos y anteras amarillos (Tabla 1). La vistosidad de algunas flores incrementa por los colores contrastantes en el tubo de la corola y el eje de la inflorescencia (ej., *Cyrilla racemiflora*, *Macairea parvifolia*, *Tibouchina fraterna*, *Sobralia liliastrum*, *Sipanea galioides*). Las brácteas representan el color adicional menos frecuente en el arbustal, sin embargo, en *Philodendron ptarianum* se combinan las flores blancas-cremosas con el interior de las brácteas espatáceas de color morado, y en *Remijia densiflora* las flores blancas se hacen más llamativas por la presencia de brácteas rojizas. Las flores organizadas individualmente están representadas en todos los colores exceptuando el verde. En contraste, la organización colectivista y las formas intermedias son más frecuentemente de colores blanco-cremosas (N = 9, 16.4%) y verdes (N = 7, 12.7%).

El diámetro de las flores varía, significativamente en relación al color, mientras que en relación al color el largo floral no mostró diferencias significativas (Tabla 2). Sin embargo, las flores verdes y las blanco-cremosas son más pequeñas en promedio (Tabla 3). El tamaño de las flores no muestra variación en relación a la simetría ni al tipo morfológico de Leppik (Tabla 2). Sin embargo, las flores irregulares son mucho más pequeñas en diámetro y longitud que las flores radiales y bilaterales (Tabla 3). La longitud de las flores tiende a incrementar desde flores haplomórficas a flores estereomórficas y zigomórficas, las cuales son similares en su longitud y diámetro (Tabla 3). En contraste, los mayores diámetros florales están asociados a flores pleomórficas y zigomórficas (Tabla 3). Ambas tendencias muestran gran variabilidad, y consecuentemente no hay una diferencia significativa (Tabla 2).

El tamaño de las flores varía significativamente de acuerdo a la organización de la unidad de polinización (Tabla 2). Las menores longitudes están asociadas a flores organizadas en forma colectivista y casos intermedios, mientras que estas medidas son comparativamente mayores para flores organizadas en forma individualista (Tabla 3).

La longevidad de las flores en el arbustal es aproximadamente de 12 horas para 35 (63.6%) especies (Tabla 1); 14 (25.4%) especies frecuentemente extienden la longevidad floral hasta dos días. En este último grupo, las flores son de consistencia membranosa (ej., Compositae, Ericaceae, Melastomataceae, Rubiaceae) o subcoriácea (Guttiferae, Theaceae, Apocynaceae, y Sarraceniaceae). Flores con una duración superior a los dos días (N = 6, 10.9%) están distribuídas en Melastomataceae, Orchidaceae, Gramineae, y Cyperaceae. En *Meriana sclerophylla* las flores sobreviven hasta tres días sin perder su organización, y simultáneamente la coloración se hace más clara. En *Catasetum discolor* y *Eriopsis biloba* (Orchidaceae) las flores son de textura subcoriácea y viven más de tres días sin cambiar su configuración.

De 55 especies estudiadas, 28 (50.9%) disponen sus flores en forma horizontal; este arreglo espacial muestra ciertas variaciones angulares (Tabla 1). El 40.0% (N = 22) de las especies presentan sus flores orientadas hacia arriba (ej., Compositae y Rubiaceae). El grupo menos numeroso (N = 5, 9.1%) tiene las flores orientadas hacia abajo (Ericaceae, Ochnaceae, y Theaceae). La relación entre la disposición de las flores y el tipo de dehiscencia de las anteras es estadísticamente significativa para 52 especies de plantas (gl = 2, $\chi^2 = 23.65$; $P < 0.001$). Las flores con anteras de dehiscencia lon-

TABLA 3. Tamaño promedio floral relativo a cuatro caracteres morfológicos florales.

Color	N	Largo $\bar{X}$ (DS)	Diámetro $\bar{X}$ (DS)
Blanco-cremoso	22	7.88 (9.29)	15.13 (19.27)
Amarillo	6	16.46 (12.19)	24.76 (7.75)
Rosado-rojo	8	19.21 (20.30)	17.26 (19.92)
Morado	10	13.20 (19.26)	18.35 (12.98)
Verde	7	2.13 (0.72)	1.26 (1.56)
Pardo	2	15.67 (6.13)	24.48 (0.50)
Simetría			
Irregular	7	2.04 (0.80)	2.32 (4.36)
Bilateral	18	15.07 (16.53)	18.41 (10.26)
Radial	30	9.95 (12.75)	17.10 (19.71)
Tipo floral (Leppik, 1977)			
Haplomórfico–Actinomórfico	7	2.57 (1.36)	0.87 (0.64)
Pleomórfico	18	6.03 (4.46)	22.08 (19.67)
Estereomórfico	22	14.35 (18.01)	14.17 (15.40)
Zigomórfico	8	13.59 (13.64)	15.16 (8.24)
Organización de la unidad de polinización			
Colectivista	5	4.18 (1.53)	1.42 (0.69)
Intermedio	15	2.44 (1.04)	3.43 (3.01)
Individualista	35	15.02 (15.64)	22.16 (17.18)

gitudinal están orientadas hacia arriba u horizontalmente (Tabla 4). En contraste, las disposición de las flores con anteras poricida es horizontal o colgante (Tabla 4).

De 49 especies con polinización biótica, la mayoría ofrece néctar exclusivamente (N = 20, 40.8%) aunque el polen es ofrecido en forma secundaria o principal en combinación con el néctar (N = 13, 26.6%). El néctar es ofrecido en dos formas: como un fluído líquido (Apocynaceae, Bignoniaceae, Ericaceae, Gentiaraceae, Humiriaceae, Rubiaceae) o como una sustancia escasa y de consistencia pegajosa adherida a la superficie secretora (ej., Aquifoliaceae, Compositae, Cyrillaceae, muchas Orchidaceae, Theaceae). Además dos especies de *Clusia* ofrecen resina como recompensa (N = 2, 4.1%). Existe una menor proporción de plantas que ofrecen polen como recompensa principal y concuerdan con aquellas especies de néctar escaso y pegajoso. En el arbustal las Melastomataceae y otras especies de plantas (ver Tabla 1) ofrecen exclusivamente polen (N = 13, 26.6%). *Philodendron ptarianum* ofrece partes florales (estaminodios), aunque también produce una sustancia pegajosa que probablemente está asociada con la adhesión del polen al cuerpo del polinizador.

RELACIÓN POLINIZADOR–PLANTA

Entre el largo del agente polinizador y el largo y diámetro de la flor no hay relación significativa. Sin embargo, cuando comparamos la relación largo/ancho de la flor y el tamaño promedio del conjunto de polinizadores, sí hay una tendencia estadísticamente significativa (N = 49; $y = 9.61x + 7.29$; $r = 0.53$; $P < 0.001$). Cuando el largo de la flor aumenta y el diámetro disminuye, el tamaño de los polinizadores incrementa.

CLASIFICACIÓN FLORAL

El análisis de agrupamiento en base a los caracteres morfológicos florales (Tabla 1) evidencia la gran diversidad floral (Fig. 1). El establecimiento

TABLA 4. Relación entre la orientación floral y el tipo de dehiscencia de las anteras.

	Orientación floral			
Tipo de dehiscencia	Horizontal N (%)	Hacia arriba N (%)	Hacia abajo N (%)	Total N (%)
Longitudinal	14 (26.92)	22 (42.31)	0 (0.00)	36 (69.23)
Poricida	11 (21.15)	0 (0.00)	5 (9.62)	16 (30.77)
Total	25 (48.08)	22 (42.31)	5 (9.62)	52

de cinco grupos artificiales a un nivel de 37% de similaridad muestran las características que se especifican a continuación. El grupo I está formado por dos especies con flores grandes tubulares de colores rosados, con una longevidad superior a un día, las cuales son polinizadas por abejas grandes y medianas. El grupo II está formado por plantas estrictamente anemófilas (Gramineae y Cyperaceae), que comparten una serie de características morfológicas y ecológicas (Tabla 1). El grupo III incluye tres especies con flores de vida larga, de colores opacos (pardos y morados), polinizadas por abejas medianas y grandes. El grupo IV es el más númeroso y heterogéneo, aunque resalta una longevidad de un día y néctar como recompensa. En este caso, se han delimitado dos subgrupos. El subgrupo IVa está conformado por plantas con flores predominantemente pequeñas, de colores blanco, amarillo, y morado, frecuentemente polinizadas por abejas medianas y pequeñas, avispas, dípteros, lepidópteros y raras veces por abejas grandes. En este subgrupo destacan especies de las familias Compositae y Rubiaceae. Las flores del subgrupo IVb son predominantemente de colores llamativos y con dimensiones superiores a las de IVa; muchas flores son tubulares y polinizadas por aves; otras son polinizadas por abejas medianas y grandes; entre las cuales destacan varias especies de las familias Melastomataceae, Ericaceae, y Orchidaceae. En el grupo V están incluidas especies con una longevidad variable, grandes diámetros, y colores predominantemente claros en combinación con colores llamativos (estambres amarillos y guías de néctar); estas están polinizadas más frecuentemente por abejas grandes.

Hay dos tendencias entre la afinidad morfológica y el comportamiento fenológico de algunas especies consideradas en cada grupo (ver Tabla 1 y Fig. 1). A un nivel menor del 90% de similaridad existen varios pares o grupos de especies con comportamiento contrastantes. Las plantas coinciden parcialmente, como *Catasetum discolor* y *Eriopsis biloba*, que comparten una especie de polinizador (*Eulaema meriana*). Otro caso similar ocurre entre *Brocchinia acuminata*, *Humiria balsamifera*, y *Phthirusa adunca*. Alternativamente los polinizadores pueden ser diferentes (Ramirez, 1989). *Remijia densiflora*, *Mikania psilostakia*, *Borreria capitata*, y *Declieuxia fruticosa* coinciden en su floración y morfología floral pero tienen polinizadores diferentes. Esta misma situación se repite en *Macairea parvifolia–Marcetia taxifolia* y en *Miconia ciliata -Siphanthera cordifolia*.

A pesar de la relativa predictibilidad de los caracteres morfológicos para delimitar los sistemas de polinización, los grupos afines de plantas en el primer análisis de agrupamiento son pobremente establecidos utilizando las especies de polinizadores como caracteres de agrupamiento (Fig. 2). El establecimiento de cuatro grupos estrictamente artificiales permiten analizar esta situación. El grupo I está formado por especies con flores predominantemente pequeñas, de colores claros (principalmente blanco), con los sistemas de polinización más diversos (de dos a siete especies) que incluyen abejas medianas y pequeñas, y raras veces grandes avispas, lepidópteros, y dípteros (Ramirez, 1989). El grupo II está representado por especies con un diámetro floral de mediano a grande; los colores son claros y predominan el rosado-rojo y el amarillo; la polinización es realizada principalmente por abejas grandes y medianas; el número de especies de polinizadores por planta varía de uno a siete. El grupo III está contituído por especies con flores de diámetro variable; los colores son más diversos y en tonalidades intensas; el número de especies polinizadoras por especie de planta varía de uno a tres, representadas principalmente por abejas grandes y medianas. El grupo IV tiene de uno a dos agentes polinizadores. Aquí destaca un subgrupo de especies anemófilas y otro polinizado por colibríes y/o abejas grandes; los colores son predominantemente llamativos (ver Tabla 1).

Discusion

Las flores pequeñas de colores claros en algunas especies pueden ser consideradas en los términos de Burtt (1961), como organización "colectivista," caracterizadas para la explotación intensiva. La inflorescencia puede funcionar como la unidad de polinización, y los polinizadores permanecen largos períodos sobre la inflorescencia (Lindsey, 1984). Las flores agrupadas en forma colectivista y formas intermedias son radialmente simétricas, de colores claros y con dimensiones significativamente menores que las flores con una organización individualista. Además, la organización y disposición de las flores en inflorescencias con una organización colectivista y formas intermedias permite simular o reemplazar grandes flores. En el arbustal hay varios grados de especialización de la inflorescencia como unidad de polinización. La mayor especialización se encuentra en Araceae y Compositae. Entre las especies más generalizadas, están *Cybianthus quelchii*, *Ilex retusa*, *Humiria balsamifera*, y *Phthirusa adunca*, las cuales pueden ser polinizadas por insectos grandes y pequeños (la flor funciona como unidad de polinización para insectos pequeños y la inflorescencia como unidad

FIGURA 1. Análisis de agrupamiento para 55 especies de plantas en base a ocho caracteres morfológicos descritos en la Tabla 1. Números basales indican especies en la Tabla 1. Números romanos indican grupos afines.

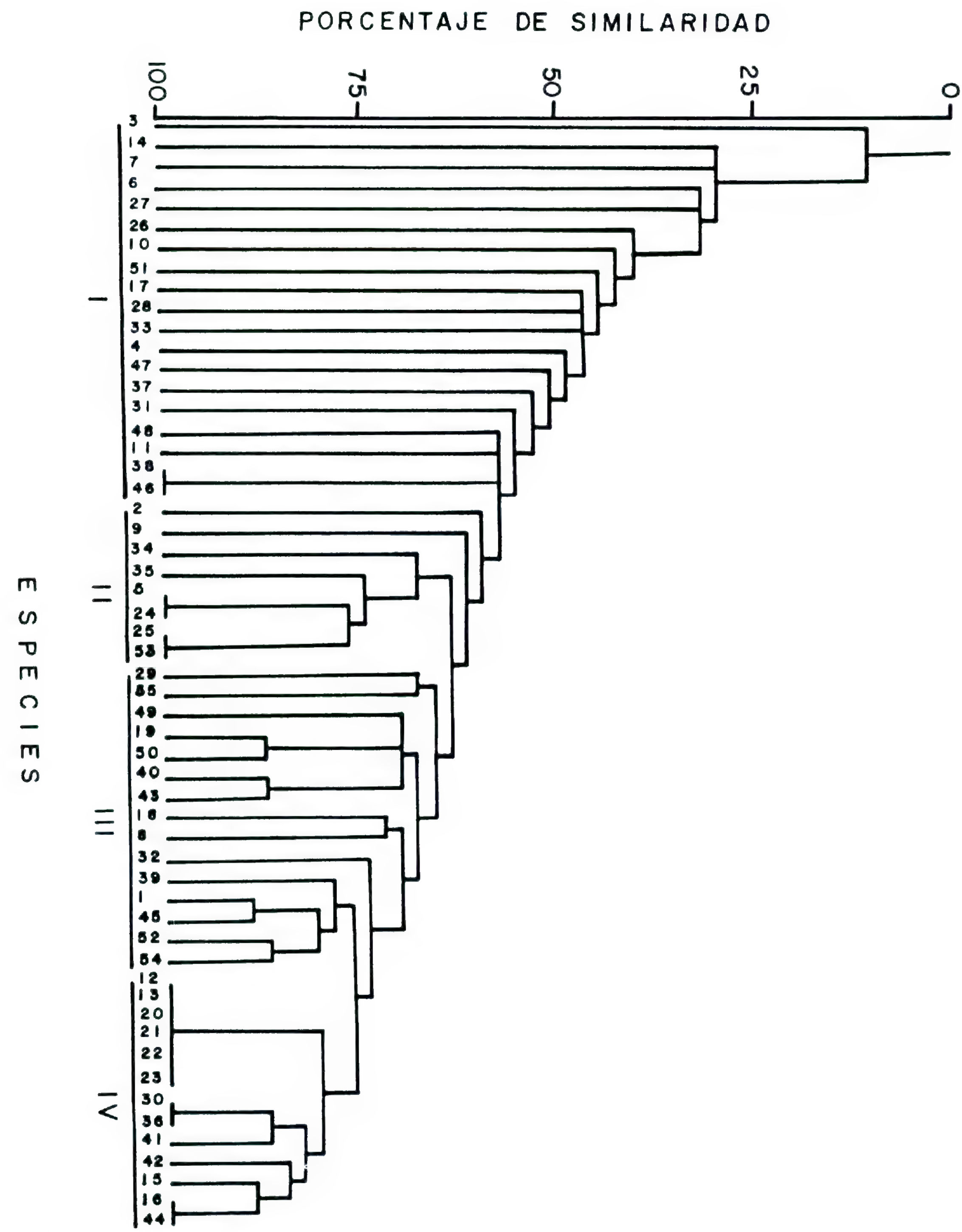

FIGURA 2. Análisis de agrupamiento para 55 especies de plantas en base a la presencia de polinizadores. Los agentes sin cargas tienen un valor de 1 y los polinizadores efectivos tienen valores de 2. Números basales indican especies de plantas en la Tabla 1. Números romanos indican grupos artificiales de afinidad.

de polinización para insectos grandes). Esto evidencia que en la comunidad arbustiva los sistemas de polinización, no sólo pueden ser caracterizados por la relación de tamaño flor—tamaño polinizador sino también por la selección de los polinizadores y la organización de la inflorescencia como unidad de polinización.

El polen y el néctar son recompensas básicas

que ofrecen las flores a los polinizadores en el arbustal. El porcentaje de especies que producen sólo néctar y en combinación con polen es similar al reportado por Percival (1974) para arbustos costeros de Jamaica. El elevado porcentaje de especies productoras de néctar ha sido relacionado con la preponderancia de visitantes consumidores de néctar (Percival, 1974). Ciertamente en el arbustal estudiado hay una alta proporción de especies ornitófilas y melitófilas productoras de néctar. Sin embargo, el 26.6% de las especies analizadas no producen néctar. La abundancia de especies anemófilas y de grupos taxonómicos adaptados a la polinización por vibración concuerdan con las proporciones encontradas. Además del polen y néctar, la resina floral es considerada como un componente crítico de ciertas comunidades tropicales (Armbruster, 1984). En el arbustal hay dos especies del género *Clusia* cuyas flores femeninas producen resina como recompensa. La escasez de néctar en *Bonnetia sessilis* y la similitud morfológica con *Clusia* especies podrían ser interpretadas como un caso de evolución convergente. La utilización indiscriminada de los polinizadores comunes, probablemente dé como resultado una estrategia que reduce el costo de recompensa en *B. sessilis*, y mantiene a las poblaciones de polinizadores asiduos a estas especies. La ventaja de especies con características florales convergentes y polinizadores comunes ha sido señalada para plantas polinizadas por colibríes (Brown & Kodric-Brown, 1979; Schemske, 1981; Kress, 1983).

El mecanismo de polinización engañosa, en la cual los polinizadores son atraídos a las flores sin recompensa, aparece muy frecuentemente en Orchidaceae (Nilsson, 1980, 1983; Dafni, 1983) y entre los árboles y lianas tropicales (Frankie et al., 1983; Haber, 1984). Este mecanismo ha sido asociado a abejas jovenes inexpertas (Nilsson, 1980) y a los polinizadores con pobre capacidad discriminativa (Dafni, 1983). La abundancia de especies con flores grandes y llamativas, y de floración simultánea sugiere que la polinización engañosa puede ser una estrategia de polinización en el arbustal. Esto es reforzado por la marcada escasez en la producción de néctar, que fue más acentuada en Orchidaceae entomófilas (*Sobralia* y *Epistephium*) y ornitófilas (*Pogonia*). Estas plantas fueron esporádicamente visitadas por los polinizadores comunes a otras especies del arbustal.

Las flores adaptadas a la polinización por abejas tienen una longevidad de un día en la mayoría de las especies arbóreas de un bosque seco de Costa Rica (Frankie et al., 1983). En el arbustal, una alta proporción de las flores viven un día. Percival (1974) encontró una alta proporción de flores restringidas a uno o medio período diurno, las cuales fueron asociadas a flores que reciben visitas por animales. La extensión en la longevidad floral podría estar asociada con la textura de las flores. Si bien todas las especies con un período diurno de actividad floral son zoófilas, en el arbustal hay especies melitófilas cuya longevidad es mayor, lo cual podría incrementar la probabilidad de polinización. Esta estrategia puede ser particularmente importante en especies con polinizadores poco predecibles. El caso más evidente ocurre en plantas anemófilas.

El tamaño de las flores es considerado como una función general del tamaño del polinizador (Opler, 1980). Lindsey & Bell (1985) señalaron que el largo del tubo y del estilo puede ser correlacionado con el tamaño del insecto. Kodric-Brown et al. (1984) destacaron la misma situación entre flores y colibríes. La longitud de la proboscis ha sido considerada una característica determinante en la selección de flores por parte de polinizadores (Macior, 1979; Ranta & Vepsäläinen, 1980; Real, 1981; Pyke, 1982) . En contraste, las flores de tubo corto permiten el fácil acceso a gran variedad de polinizadores (Kephart, 1983). Sin embargo, existen excepciones que no apoyan la hipótesis de repartición del recurso (Macior, 1974; Bauer, 1983; Roubik & Buchmann, 1984).

En el arbustal estudiado, la selección de las flores en relación al diámetro y el largo del tubo de la corola no apoyan la correlación entre tamaño flor y tamaño insecto, pero la combinación del tamaño floral expresado por la relación largo/diámetro sí se aproxima a reflejar el tamaño promedio de los insectos polinizadores. Esta relación destaca que solo la combinación de las dos medidas florales estan correlacionadas con la longitud promedio del conjunto de polinizadores. Flores con diámetros y longitudes similares, son predominantemente polinizadas por insectos pequeños, mientras que las flores cuya longitud es mayor que el diámetro son polinizadas por insector grandes. La validez de esta relación está sujeta a excepciones, entre las cuales destacan las flores poco profundas y con grandes diámetros (ej., *Clusia* spp.) y las flores pequeñas donde la inflorescencia es la unidad de polinización; ambasson polinizadas por insectos grandes y pequeños.

Las flores entomófilas del arbustal con dehiscencia poricida son polinizadas por abejas vibrátiles, aunque *Marcetia taxifolia* es visitada por avispas y mariposas. La polinización en plantas con anteras poricidas pero visitadas por agentes no vibrátiles puede ser explicada parcialmente por el

hecho de que el viento (el cual es muy fuerte en el arbustal) puede facilitar la dispersión del polen (Tomlinson et al., 1979). Alternativamente, algunos insectos pueden morder las anteras y así colectar el polen (Buchmann & Buchmann, 1981; Renner, 1983). Cuando los agentes visitantes son tanto vibrátiles como no vibrátiles, las visitas previas por agentes vibrátiles depositan abundante polen por toda la flor, lo cual podría contribuir a que otros agentes efectúen la polinización.

La orientación de las flores respecto al sustrato puede ser considerada de gran utilidad en el estudio de los sistemas de polinización y del ambiente. Las flores polinizadas por agentes vibrátiles pueden estar orientadas en cualquier posición respecto al sustrato (Buchmann, 1978). El 9.1% de las flores del arbustal están orientadas hacia abajo; además, las corolas son urceoladas o subglobosas (constricción distal del tubo de la corola), o los pétalos están plegados a los estambres (*Sauvagesia angustifolia*). Esta organización floral conduce a que el polen en estas especies es depositado pasivamente sobre los pétalos y retenido principalmente en la constricción de la corola. En este sentido, la colección de polen por agentes no vibrátiles (aves, dípteros, y abejas) puede ser efectiva. Además, esta orientación floral ha sido asociada con la selectividad por parte del polinizador (Tomlinson et al., 1979; Sullivan, 1984), complementariamente, podría reducir la interferencia de la lluvia, la cual es frecuente en el área de estudio.

El comportamiento fenológico de las plantas con características florales similares tiende a estar separado temporalmente para evitar la competencia por los polinizadores (Gentry, 1974; Frankie et al., 1983; Whitney, 1984). Las especies con caracteres morfológicos florales ligeramente uniformes pueden estar sometidas a la carencia de reconocimiento por parte de los polinizadores (ej., Sullivan, 1984). Los sistemas de polinización raras veces son idénticos (especies de polinizadores) en las especies de plantas del arbustal de la Gran Sabana (Ramirez , 1989). Algunas especies de plantas con caracteres morfológicos similares pueden tener polinizadores comunes o diferentes. Esto sugiere que la similitud morfológica de los caracteres florales considerados en este trabajo no es evidencia directas para suponer especies de polinizadores comunes. Sin embargo, los grupos afines de especies de plantas, basados en los caracteres morfológicos, permiten destacar que hay mayor similitud en relación a los grandes grupos de polinizadores en comparación con la afinidad taxonómica. Claramente, en casos donde hay una alta especialización a un solo agente polinizador (ej., anemofilia), las plantas son categorizadas en grupos homogéneos de acuerdo a los caracteres morfológicos florales *y* a su posición sistemática (ej., Cyperales).

La delimitación de grupos de plantas en base a los agentes polinizadores permite destacar que no existen grupos claramente definidos por las especies de polinizadores, sino más bien un conjunto de plantas que superponen algunas características morfológicas comunes, asociadas a ciertos grupos de visitantes: las especies polinizadas por pequeños insectos con flores pequeñas y colores claros y las plantas polinizadas por abejas medianas y grandes con flores grandes y de colores llamativos. La variabilidad observada en este grupo de plantas podría estar asociada a la diversidad del conjunto de especies visitantes. En contraste, las especies ornitófilas y anemófilas están fuertemente relacionadas en sus caracteres morfológicos florales y agentes polinizadores.

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THE SYSTEMATICS OF *SOLANUM* SECTION *ALLOPHYLLUM* (SOLANACEAE)[1]

Lynn Bohs[2]

ABSTRACT

Three species of *Solanum* are included in a new section, *Solanum* sect. *Allophyllum*. Two of the species, *S. allophyllum* and *S. mapiriense*, have been previously known; the third, *S. morellifolium* Bohs, is described as new. The combination of characters exhibited by members of this section, such as unbranched hairs, 2–3-leaved sympodial units, simple leaves with decurrent bases, and tapered anthers, is unique to this group and does not agree well with any existing subgenus of *Solanum*.

A group of three species first attracted my attention during monographic work on the solanaceous genus *Cyphomandra* Sendtn. *Solanum allophyllum* (Miers) Standl., the most widespread and best-known species of the section, had been placed by various workers in *Cyphomandra* and in *Solanum*. Determination of the true affinities of this species entailed an examination of the validity of the characters separating the two genera. An account of the morphology of this species and its resultant exclusion from *Cyphomandra* is given in a separate paper (Bohs, 1989).

Bitter (1914) first noted the similarities between *S. allophyllum* (his *S. ellipsoideibaccatum* Bitter) and *S. mapiriense* Bitter (his *S. phytolaccoides* (Rusby) Bitter), but he did not create a formal taxonomic category to include them. Child (1984) erected sect. *Allophylla* to contain these two species and regarded the new section as belonging to *Cyphomandra* rather than to *Solanum*. He also surmised that *Cyphomandra chlorantha* Rusby belonged to sect. *Allophylla*, but Bohs (1986) confirmed that it belongs in *Cyphomandra* and that it has no close relationship to *S. allophyllum* or *S. mapiriense*. A recent analysis of *S. allophyllum* (Bohs, 1989) indicates that this species should be placed in *Solanum* instead of *Cyphomandra*. Accordingly, sect. *Allophylla* is here removed from *Cyphomandra* and placed in *Solanum*.

All three species of *Solanum* sect. *Allophyllum* share the following combination of characters: (1) upright herbs or shrubs (up to 2 m tall); (2) 2–3-leaved sympodial units; (3) vegetative parts densely covered with "sand-punctae" (idioblasts containing crystal sand); (4) membranaceous leaf blades, usually with decurrent bases and winged petioles; (5) unbranched, few-flowered, relatively short inflorescences; (6) flowers with usually white or greenish white membranaceous corollas; (7) stamens with glabrous filaments, distally tapered anthers, and very small terminal pores; (8) glabrous, filiform styles with small truncate stigmas; and (9) glabrous, globose to ellipsoidal fruits with obtuse apices. Additional characters may further distinguish the section, but these are as yet imperfectly known for all three species. For instance, *S. allophyllum* and *S. mapiriense* have light-colored corollas and anthers both with darker spots at the base, but such spots have not been observed in *S. morellifolium*. Also, the fruits of *S. allophyllum* have a distinctive color and shape, being white to light orange marked with dark green or purple longitudinal stripes and being ovoid to ellipsoidal in outline but flattened on opposite sides (Bohs, 1989). The color and shape of mature fruits of *S. mapiriense* and *S. morellifolium* are unknown.

Most of the character states that define sect. *Allophyllum* are found in many other sections of *Solanum* and are probably plesiomorphic. These include (1) herbaceous habit; (2) exclusively simple, unbranched hairs; (3) absence of prickles; (4) presence of sand-punctae; (5) cuneate and decurrent leaf bases; (6) glabrous filaments; (7) glabrous, filiform styles with small truncate stigmas; (8) gla-

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brous, obtuse fruits; (9) stone granules in the fruits; and (10) small, flattened seeds. Probable derived character states manifested by members of the section include (1) tapered anthers with small terminal pores; (2) 2–3-leaved sympodial units; and (3) self-compatible breeding system (known only for *S. allophyllum*). The evolutionary significance of the laterally compressed fruits seen in *S. allophyllum* (and possibly present in the other two species) is uncertain, but compressed fruits occur in other subgroups of *Solanum*, such as the subgenera *Potatoe* (G. Don) D'Arcy and *Bassovia* (Aubl.) Bitt. The distribution of flattened fruits among other solanaceous genera is unknown to me. Perhaps this character is relatively insignificant taxonomically and may be related to the enlargement of the ovary wall and septum during fruit development.

In summary, sect. *Allophyllum* seems to combine a host of primitive features with a few seemingly derived character states, most notably tapered anthers.

Placement of the Section Within *Solanum*

Solanum is one of the largest genera of flowering plants, containing an estimated 1,500 species (D'Arcy, 1979; Hunziker, 1979). Substantial taxonomic problems still exist with regard to *Solanum* and related genera. At present, *Solanum* is loosely defined and consists of plants with poricidally dehiscent anthers that lack the specialized features of associated segregate genera, such as enlarged anther connectives in *Cyphomandra* Sendtn., sterile anther beaks in *Lycopersicon* Mill., and distinctive calyx morphology in *Lycianthes* (Dun.) Hassl. Although each of these segregate genera may be monophyletic, monophyly has not been established for *Solanum*. Poricidal anther dehiscence may have evolved more than once in *Solanum* and its allies, and may thus not be a synapomorphy uniting these taxa. Certainly our understanding of phylogenetic relationships within *Solanum* is hampered by the lack of basic taxonomic and morphological information for many subgenera and sections within the genus. It seems inevitable that *Solanum* will be broken up into smaller monophyletic genera, but taking such a step now would be premature based on our current state of knowledge. The infrageneric classification of *Solanum* and the boundaries between *Solanum* and its related genera have not been firmly established, and the taxonomy of this group is likely to remain in a state of flux for many years to come.

The placement of sect. *Allophyllum* in *Solanum* is enigmatic. No existing group in *Solanum* has the combination of tapered anthers, simple hairs, upright habit, simple leaves, and spinelessness seen in sect. *Allophyllum*. In fact, the anthers of this group resemble those of some species of *Lycianthes*, but sect. *Allophyllum* does not have the truncate calyx with subapical lobes, reduced inflorescences, and large stone cell aggregates in the fruits that distinguish *Lycianthes* (D'Arcy, 1986). Section *Allophyllum* may represent a new genus with characters intermediate between *Solanum* and *Lycianthes*, but no synapomorphies are known that distinguish sect. *Allophyllum* from *Solanum*. Given the possible polyphyly, or at least paraphyly, of *Solanum*, sect. *Allophyllum*, differentiated on the basis of a combination of characters but with no obvious synapomorphies, must be placed in *Solanum*. Further work on generic limits between *Solanum* and its allies will undoubtedly shed light on the proper generic placement of this section. Additional problems surface when the affinities of sect. *Allophyllum* within *Solanum* are considered, because the infrageneric classification scheme in *Solanum* leaves much to be desired.

Several attempts have been made to divide *Solanum* into subgenera and sections (e.g., Dunal, 1852; Seithe, 1962; Gilli, 1970; Danert, 1970; D'Arcy, 1972). The most widely used recent scheme is that of D'Arcy (1972), who accepted seven subgenera of *Solanum*, in a classification with basic elements derived from earlier literature. I will refer exclusively to his classification in the discussion below.

Although many well-defined sections can be discerned within *Solanum*, the circumscription of subgenera is more problematic. Most of the subgenera consist of one or several well-defined or well-studied sections along with a number of sections whose affinities are less certain. Thus, D'Arcy's subgenera are often clearly defined with respect to one or a few component sections, but the boundaries between the sugenera are less clear when all the associated sections are considered.

The large number of species in *Solanum* and the relative paucity of adequate taxonomic treatments for many infrageneric groups hampers understanding the genus. Because I lack the facilities for an exhaustive survey of morphology and variation in the entire genus, it is possible that I have overlooked existing groups in *Solanum* that might be allied with sect. *Allophyllum*. Nevertheless, I will attempt to enumerate the possibilities for placement of sect. *Allophyllum* within the existing subgenera of *Solanum* as I understand them.

Section *Allophyllum* probably does not belong to the subgenera *Archaesolanum* Marz. (aneu-

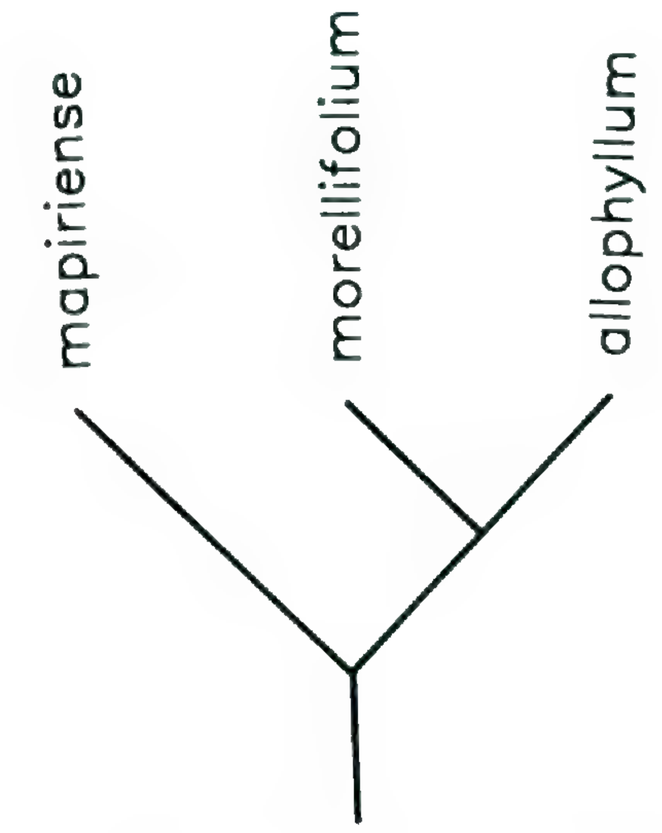

FIGURE 1. Hypothesis of phylogenetic relationships in *Solanum* sect. *Allophyllum*.

ploid-polyploid South Pacific species), *Lyciosolanum* Bitt. (restricted to a single South African species, *S. aggregatum* Jacq., with sessile inflorescenses, short shoots, and very long filaments), or *Brevantherum* (Seithe) D'Arcy (exemplified by sect. *Brevantherum* Seithe, which contains species with entire leaves, elliptic to oblong anthers with blunt apices, and stellate hairs).

Bitter (1913) and Morton (1944) postulated an alliance of *S. allophyllum* with subg. *Leptostemonum* (Dun.) Bitt. because both groups have tapered anthers with small terminal pores. Such a relationship is doubtful, however, because all species of sect. *Allophyllum* lack the stellate hairs and prickles characteristic of subg. *Leptostemonum*.

Members of sect. *Allophyllum* resemble vegetatively those of sect. *Solanum* of subg. *Solanum* and have often been identified as members of sect. *Solanum* in herbaria. Both sections contain herbaceous plants with ovate to ellipsoidal leaf blades having decurrent bases; usually extra-axillary, relatively few-flowered inflorescences with an obvious peduncle; and often small aggregates of stone cells in the fruits. The lobed leaves of *S. allophyllum* also resemble those of *S. dulcamara* L., which D'Arcy placed in subg. *Potatoe* (G. Don) D'Arcy but which probably belongs to subg. *Solanum*. However, all species of subg. *Solanum* have oblong to ellipsoidal anthers that dehisce by large terminal pores opening into longitudinal slits rather than the tapered anthers with small pores that characterize sect. *Allophyllum*. Thus the resemblance of sect. *Allophyllum* to members of subg. *Solanum* appears to be superficial and based only on vegetative characters.

Section *Allophyllum* is not easily accommodated in subg. *Potatoe*. Although some members of this subgenus have more or less tapered anthers, they are also dehiscent by large terminal pores that frequently develop into longitudinal slits. Many species of this group have twining stems and pinnately compound leaves, and self-incompatibility is common. None of these attributes suggests a relationship with sect. *Allophyllum*.

The remaining subgenus, subg. *Bassovia*, also does not appear to be a good candidate. Most members of this group have stout anthers with large apical pores that later open into longitudinal slits, and inflorescences located in leaf axils. These characteristics are not seen in sect. *Allophyllum*. Tapered anthers occur in *S. reptans* Bunb. of the monotypic sect. *Herposolanum* Bitt., but they open by longitudinal slits, and this species has no further morphological resemblance to sect. *Allophyllum*. (The inclusion of *Solanum reptans* in subg. *Bassovia* is itself doubtful.) Laterally compressed fruits occur in some species of this subgenus, but so little is known of the distribution and development of this character that it is not possible to determine whether this is an important link between sect. *Allophyllum* and subg. *Bassovia*.

The preceding considerations indicate that sect. *Allophyllum* does not fit well into any of the existing subgenera of *Solanum*. The group certainly deserves sectional rank, but given the problems already noted for its placement at both the generic and infrageneric levels, I am hesitant to create a new subgenus for it now.

INFRASECTIONAL RELATIONSHIPS

Within the section, *S. allophyllum* is most likely the most advanced species, exhibiting a suite of possible derived characters, such as pinnately lobed leaves, inflorescences situated in branch forks, rotate-stellate corollas, and large, ellipsoidal fruits. *Solanum mapiriense* may be the most primitive element of the section, exhibiting none of the derived features mentioned above for *S. allophyllum*. *Solanum morellifolium* shares with *S. allophyllum* few-flowered inflorescences, rotate-stellate corollas, and small ovate-elliptic leaf blades; on the other hand, *S. morellifolium* resembles *S. mapiriense* by having extra-axillary inflorescences, small globose fruits, and by lacking pinnately lobed leaves. The presence of gland-tipped finger hairs (unbranched multicelled stalks with a unicelled glandular tip) on the stems and inflorescences of *S. mapiriense* and some collections of *S. morellifolium* may be an indication of the relatively primitive status of these species, for gland-tipped finger hairs are thought by Seithe (1979), based on her ontogenetic studies, to be the most primitive hair type in *Solanum*. Finger hairs (without glandular tips) and multicellular glands (unicelled stalks with mul-

ticelled glandular tips) are the hair types found on the mature foliage and stems of *S. allophyllum*.

A preliminary hypothesis of the relationships among these three species is given in Figure 1. This should be interpreted only as a hypothesis for further examination and testing. A rigorous cladistic analysis can be attempted only when the proper placement of sect. *Allophyllum* within *Solanum* is known, when further information is gathered for many of the poorly characterized groups within the genus, and when appropriate hypotheses can be made concerning character polarity within and among the various lineages of *Solanum*.

Taxonomic Treatment

Solanum section **Allophyllum** (Child) Bohs, comb. nov. *Cyphomandra* section *Allophylla* Child, Feddes Repert. 95: 292. 1984. Type species: *Solanum allophyllum* (Miers) Standl.

Herbae vel frutices fere glabra vel pilis simplicibus, omnibus partibus vegetativis abundanter areni-punctatis. Sympodia 2–3-foliata. Laminae foliorum simplices lobatae vel non lobatae basi subcordatae truncatae vel cuneatae plerumque in petiolum decurrentes. Inflorescentiae extra-axillares vel in furcis ramorum locatae non ramosae minus quam 10 cm longae floribus paucis; pedicelli 3–9 mm longi basi articulati. Corolla alba vel viridi-alba saepe basi maculis fuscatis. Stamina circum stylum conniventia; filamenta brevissima; thecae antherarum basi auriculatae apicem versus valde attenuatae, poris duobus apicalibus minimis dehiscentes. Stylus glaber filiformis; stigma truncatum. Bacca glabra ovoidea vel ellipsoidea apice obtusa.

Herbs or *shrubs* up to about 2 m tall. *Branches* glabrous to sparsely puberulent, abundantly sand-punctate. *Leaves* 2–3 per sympodial unit, the blades simple, lobed or unlobed, chartaceous to membranaceous, abundantly sand-punctate, the apex acuminate, the base subcordate to truncate or cuneate, decurrent along petiole, the midrib and major lateral veins prominent abaxially; petioles winged, glabrous to minutely puberulent, especially in adaxial channel. *Inflorescence* extra-axillary or located in a branch fork, unbranched, with up to 15 flowers, shorter than 10 cm long; pedicels 3–9 mm long, articulated at the base. *Calyx* membranaceous, veiny and sand-punctate. *Corolla* white or greenish (possibly blue?), usually with darker spots at the base, membranaceous, veiny and sand-punctate, glabrous to sparsely puberulent abaxially and adaxially, the margin glabrous to minutely tomentose, the apices acute. *Stamens* tightly connivent around style; filaments inserted about 1 mm above the corolla base, the free part of the filaments shorter than 1 mm and much shorter than the anthers; anther thecae narrowly triangular, strongly tapered distally, sagittate at base, thickened abaxially in proximal half, the pores very small and directed distally. *Ovary* glabrous, ca. 1–3 mm long, 1–2 mm diam.; style glabrous, filiform, less than 0.5 mm diam., longer than the ovary; stigma truncate, the same diameter as style. *Fruit* glabrous, obtuse at apex, ovoid or ellipsoidal, laterally compressed in *S. allophyllum* and possibly also in the two other species.

Key to Species of *Solanum* Section *Allophyllum*

1a. Leaf blades unlobed, elliptic, 10–27 cm long, 4–12 cm wide; inflorescences 8–15-flowered; corolla stellate, the lobes 6–8 mm long and 3–4 mm wide ..... 1. *Solanum mapiriense*

1b. Leaf blades lobed or unlobed, the unlobed leaves with blades ovate, ovate-elliptic, or triangular, 2.5–17 cm long, 1.3–7.5 cm wide; inflorescences 3–7-flowered; corolla rotate-stellate, the lobes 2–6 mm long and 1.5–3 mm wide.

2a. Inflorescences 0.5–2.5 cm long; peduncles 0.3–1.5 cm long; corolla radius 4–5 mm long, the tube 1–2 mm long, the lobes 2–4 mm long; anther thecae 2.5–4 mm long; fruits globose, ca. 1 cm long and 1 cm in diameter; eastern Peru and adjacent Bolivia ..... 2. *Solanum morellifolium*

2b. Inflorescences 1.5–7 cm long; peduncles 1–4.5 cm long; corolla radius 7–10 mm long, the tube 3–4 mm long, the lobes 4–6 mm long; anther thecae 5–6 mm long; fruits ovoid or ellipsoidal, 2.5–4 cm long, 1.5–2.5 cm wide; Central America and northwestern South America ..... 3. *Solanum allophyllum*

1. Solanum mapiriense Bitter, Repert. Spec. Nov. Regni Veg. 11: 16. 1912. TYPE: Bolivia. La Paz: San Antonio near Mapiri, 850 m, Dec. 1907, *Buchtien 1434* (lectotype, US #1399273, here designated; isolectotype, US #1175838).

Bassovia phytolaccoides Rusby, Bull. N.Y. Bot. Gard. 4: 317. 1907. *Solanum phytolaccoides* (Rusby) Bitter, Repert. Spec. Nov. Regni Veg. 13: 172. 1914, non *S. phytolaccoides* C. H. Wright, 1894. *Cyphomandra phytolaccoides* (Rusby) Child, Feddes Repert. 95: 292. 1984. TYPE: Bolivia. La Paz: Tipuani-Guanai, Dec. 1892, *Bang 1740* (lectotype, NY, here designated; isolectotypes, A, BM, E, GH, NY, US). Figure 2.

Herb or *shrub* ca. 1–2 m tall. *Branches* glabrous to sparsely puberulent with gland-tipped finger hairs. *Leaves* 2 per sympodial unit, the blades unlobed, elliptic, glabrous to sparsely puberulent or pubescent adaxially, nearly glabrous abaxially, (5–)10–27 cm long, (2–)4–12 cm wide, the length : width ratio ca. 2–3 : 1; major veins 5–11 on each side; petioles 1–5 cm long. *Inflorescence* extra-axillary, 8–15-flowered, 2–6 cm long; peduncle

FIGURE 2. Isolectotype of *Bassovia phytolaccoides* (= *Solanum mapiriense*) (*Bang 1740* BM).

1–3 cm long; rachis 1–4 cm long; pedicels 5–9 mm long, in fruit 7–9 mm long, spaced (1–)2–6 mm apart. Peduncle, rachis, and pedicels sparsely to moderately puberulent with curled gland-tipped finger hairs. *Calyx* glabrous to moderately glandular-puberulent, the radius 2 mm, the margin nearly entire with very shallow obtuse lobes. *Corolla* white to cream or greenish white with green spots at base (with deep blue center *fide* Rusby), stellate, the radius 8–10 mm, the tube 1–3 mm long, the lobes 6–8 mm long, 3–4 mm wide, elliptic to ovate, the apex short-tomentose. *Stamens* ca. 6 mm long; anther thecae yellow or white with green spots at base, (darker at the base *fide* Rusby), narrowly triangular, ca. 4–6 mm long, 1.5–2 mm wide at base, ca. 0.5 mm wide at apex. *Style* ca. 6 mm long, 0.2–0.5 mm diam.; stigma 0.2–0.5 mm diam. *Fruit* globose, 5–9 mm long, 4–9 mm diam. (when immature?), the color when ripe unknown; presence of stone cell aggregates in mesocarp unknown (not present according to Bitter, 1912); seeds unknown.

Distribution. Known only from moist forest of western Bolivia in the Province of La Paz, 850–1,700 m (Figure 3).

Additional specimens examined. BOLIVIA. LA PAZ: Mapiri region, San Carlos, 850 m, 12 Dec. 1926, *Buchtien 1259* (NY); Prov. Nor Yungas, 10 km by road N and above Caranavi, ca. 15°47′S, 67°32′W, 1,400 m, 1 Nov. 1984, *Nee & Solomon 30305* (NY, UT); Prov. Nor Yungas, 4.6 km below Yolosa, then 19.1 km on road up the Río Huarinilla, 16°12′S, 67°53′W, 1,700 m, 12 Nov. 1982, *Solomon 8757* (NY).

This species differs from the others of the section by its large elliptic leaves and relatively large stellate corollas with long lobes. The fruits are small

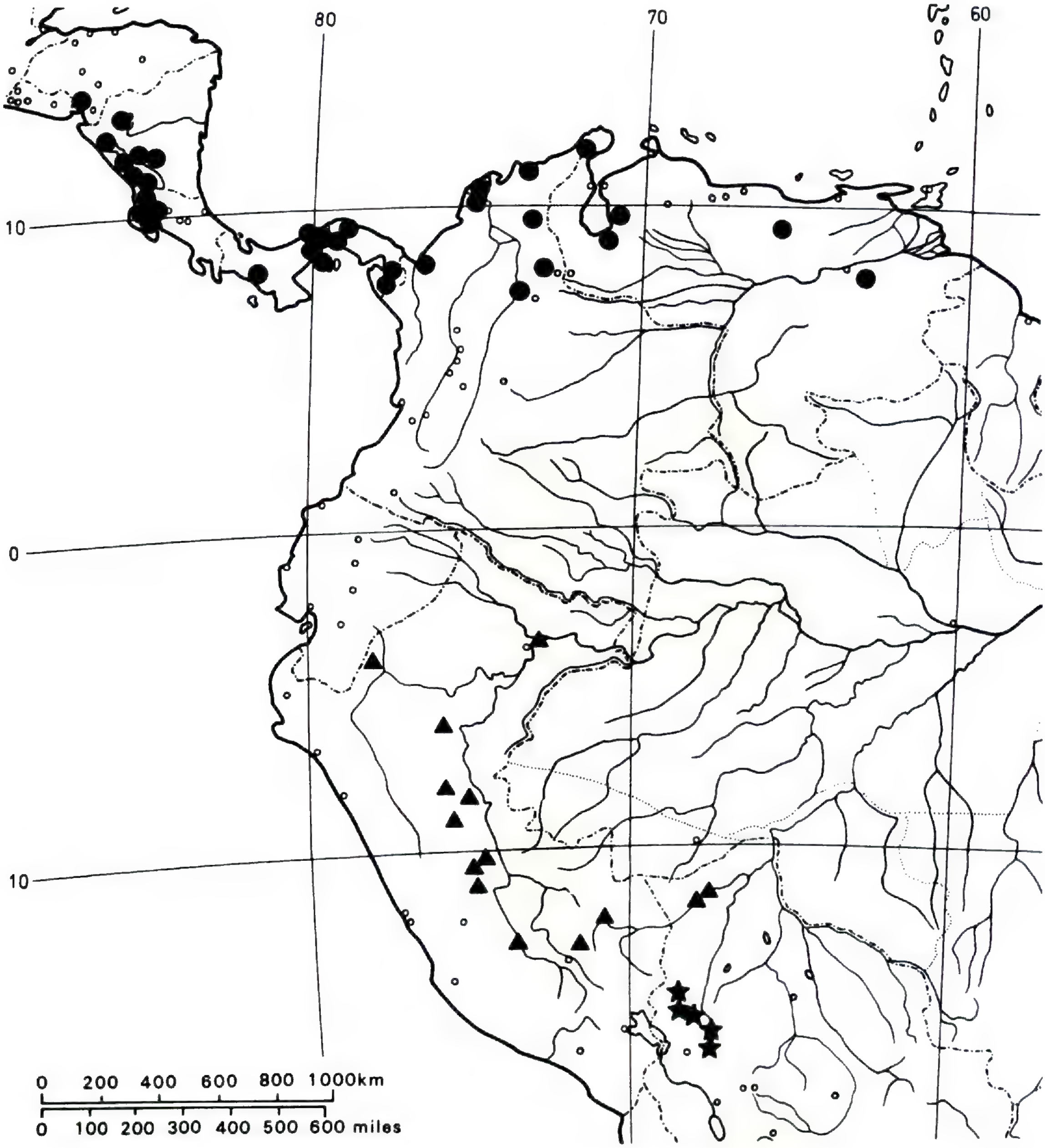

FIGURE 3. Distribution of *Solanum* sect. *Allophyllum*. Dots = *S. allophyllum*. Triangles = *S. morellifolium*. Stars = *S. mapiriense*. (Base map copyright 1979 by the University of Utrecht.)

and globose like those of *S. morellifolium*. Thus far *S. mapiriense* has only been collected from a restricted area of western Bolivia.

Although it is not possible to determine fruit shape from the herbarium specimens available, Rusby's description mentions that the fruits of *S. mapiriense* are slightly depressed and have two grooves. Laterally compressed fruits may therefore be characteristic of this species as well as of *S. allophyllum*.

Solanum mapiriense is the correct name for this species, as the combination *Solanum phytolaccoides* (Rusby) Bitter is a later homonym of *S. phytolaccoides* C. H. Wright.

Rusby did not specify the holotype for his *Bassovia phytolaccoides*, so a specimen at NY bearing his annotation has been chosen as the lectotype.

Bitter cited two syntypes for *S. mapiriense*, *Bang 1740* and *Buchtien 1434*. He stated in the protologue that he examined these specimens in

"herb. Buchtien." Although most of Buchtien's collections are at US, duplicates exist elsewhere, so "herb. Buchtien" does not precisely reveal the location of his types. The only specimens I have seen with a definite indication that Bitter examined them are *Buchtien 1434* (US #1399273) and *Bang 1740* (US #1175839) at US. The former sheet bears the annotation "*Solanum mapiriense* Bitter (det. Bitter)," but the handwriting does not appear to be Bitter's. Furthermore, the label data do not precisely match that of the protologue; on the label it says "an Waldwegen," whereas the protologue reads "in viis silvaticis." The latter sheet has an annotation label in Bitter's writing in the packet. However, this label reads "*Solanum phytolaccoides* (Rusby) Bitt.," with *Bassovia phytolaccoides* Rusby and *Solanum mapiriense* Bitter given as synonyms. As Bitter was not aware of Rusby's name when he described *S. mapiriense* in 1912, he must have examined this specimen at a later date, and it cannot be considered the type. In the absence of any better alternative candidates for the type of *S. mapiriense* Bitter, I have designated *Buchtien 1434* at US as the lectotype.

2. Solanum morellifolium Bohs, sp. nov. TYPE: Peru. Ucayali: Prov. Coronel Portillo, Bosque von Humboldt Experimental Station, carretera marginal, km 86 toward Puerto Bermudez, 75°05′W, 8°45′S, ca. 330 m, 18 Apr. 1982, *D. Smith, Angulo & Lynch 1337* (holotype, MO; isotype, NY). Figure 4.

Herba fere glabra. Laminae foliorum non lobatae ovatae basi decurrentes. Inflorescentiae extra-axillares breves 3–7 floribus praeditae. Corolla rotato-stellata viridi-alba, lobi 2–4 mm longi. Thecae antherarum 2.5–4 mm longae. Stylus circa 3 mm longus. Bacca globosa circa 1 cm diametro.

Herb or *shrub* 0.5–1 m tall. *Branches* glabrous to very sparsely puberulent, rarely moderately puberulent with gland-tipped finger hairs. *Leaves* 2–3 per sympodial unit, the blades unlobed, ovate to ovate-elliptic or ± triangular, glabrous to sparsely puberulent adaxially and abaxially, 2.5–17 cm long, 1.3–7 cm wide, the length : width ratio ca. 2 : 1; major veins 4–8 on each side; petioles 0.5–7 cm long. *Inflorescence* extra-axillary, 3–7-flowered, 0.5–2.5 cm long; peduncle 3–15 mm long; rachis 3–10 mm long; pedicels 3–7 mm long, in fruit 5–8 mm long, spaced 1–4 mm apart. Peduncle, rachis, and pedicels glabrous to very sparsely and minutely puberulent, rarely moderately puberulent with gland-tipped finger hairs. *Calyx* glabrous, the radius 1–2 mm, the margin nearly entire except for 5 very short obtuse lobes or with deltate lobes ca. 0.5–1 mm long and 1 mm wide. *Corolla* white or greenish white (blue *fide Smith et al. 1337*), rotate-stellate, the radius 4–5 mm, the tube 1–2 mm long, the lobes 2–4 mm long, 1.5–2 mm wide, triangular, the apex short-tomentose. *Stamens* 3.5–4 mm long; anther thecae yellow or white, 2.5–4 mm long, 1–1.5 mm wide at base, 0.3–0.5 mm wide at apex, triangular. *Style* ca. 3 mm long, ca. 0.2–0.5 mm diam. stigma ca. 0.2–0.5 mm diam. *Fruit* globose, 7–12 mm long, 6–12 mm diam. (when immature?), green or red (*Kayap 750*) or green with purple lines (*Smith et al. 1337*; *Knapp & Mallet 6642*); mesocarp with small aggregates of stone cells; seeds ca. 2 mm long, 1.5 mm wide.

Distribution. Forests or forest clearings of eastern Andean slopes and adjacent lowlands in Peru and Bolivia, 100–1,300 m (Fig. 3).

Vernacular names. Chuagkáteme (*Kayap 750*).

Additional specimens examined. PERU. AMAZONAS: 12–15 km N of Huampami, 1,200 m, 2 Oct. 1972, *Berlin 156* (MO); Quebrada Huampami, Río Cenepa, 15 May 1973, *Kayap 750* (MO). AYACUCHO: Río Apurimac valley, near Kimpitiriki, 400 m, 10 May 1929, *Killip & Smith 22972* (NY, US). CUZCO: Prov. La Convención, Sahuayaco, Río Chalpimayo above Pacchar, 3,850 ft., 25 Jan. 1975, *Plowman & Davis 4858* (GH). HUÁNUCO: near Tingo María, ca. 600 m, 1 June 1977, *Hart 601* (A); Prov. Pachitea, Dist. Honoria, Bosque Nacional de Iparía, cerca del campamento Miel de Abeja, 300–400 m, 2 Mar. 1967, *Schunke 1706* (NY). JUNÍN: E of Quimiri Bridge, near La Merced, 800–1,300 m, 1–3 June 1929, *Killip & Smith 24015* (NY, US). LORETO: Prov. Maynas, trail from Indiana on Río Amazonas to Río Napo, 200 m, 24 May 1978, *Gentry et al. 22172* (MO); near Yurimaguas, 180–200 m, Nov. 1982, *Ochoa & Hooker 14885* (US). MADRE DE DIOS: Prov. Manú, Parque Nacional Manú, Cocha Cashu Station, 71°23′W, 11°53′S, 350 m, 12 Sep. 1986, *Foster 11363* (NY); same locality, 71°0′W, 11°45′S, 400 m, 15 Aug. 1986, *Núñez 5724* (NY). PASCO: Oxapampa, km 15 of Palcazu Road (km 73 Villa Rica–Iscozacin-Pto. Mairo) along Río Palcazu, 10°21′S, 75°10′W, 380 m, 17–18 Aug. 1984, *Knapp & Mallet 6642* (NY, US); Río Palcazu Valley, Iscozacin, 7 Oct. 1984, *Whalen & Salick 854* (NY). BOLIVIA. PANDO: Prov. Madre de Dios, along Río Madre de Dios, upstream and 22 km WSW of Florencia, 11°30′S, 67°34′W, 135 m, 23 Aug. 1985, *Nee 31505* (NY); Prov. Manuripi, along Río Madre de Dios, 3 km W of Humaita, 12°1′S, 68°18′W, 150 m, 30 Aug. 1985, *Nee 31658* (UT).

This species closely resembles *S. allophyllum*, but *S. morellifolium* has much smaller inflorescences, flowers, and fruits. The lobed leaves often seen in *S. allophyllum* apparently do not occur in this species. Although most collections are nearly glabrous, a few have glandular-puberulent inflorescence axes like those of *S. mapiriense*.

The specific epithet refers to the great similarity

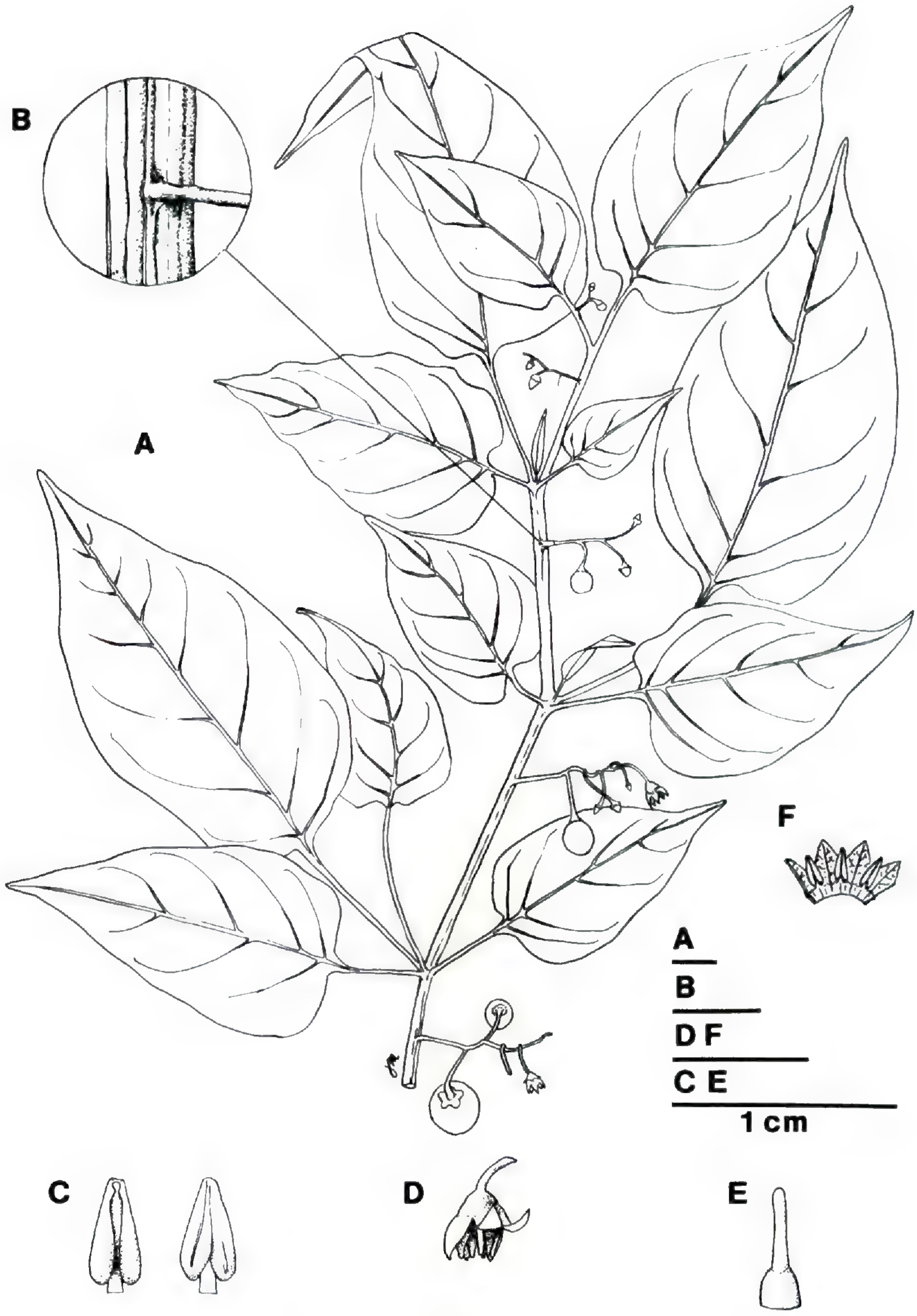

FIGURE 4. *Solanum morellifolium*.—A. Crown branch.—B. Stem and peduncle.—C. Stamens (left, abaxial view; right, adaxial view).—D. Flower.—E. Gynoecium—F. Corolla opened to show insertion of stamens. (A–E based on *Smith et al. 1337* MO; F based on *Nee 31505* NY.)

of the leaves of this species to those of *Solanum* sect. *Solanum*, which was formerly known as *Morella* or *Maurella* until the name was changed to sect. *Solanum* in accordance of the rules of botanical nomenclature (Seithe, 1962).

Data from *Knapp & Mallet 6642* indicate that Ithomiine butterflies of the genus *Thyridia* oviposit on *S. morellifolium*. With this exception, all the known larval food plants for *Thyridia* belong to *Cyphomandra* (Drummond, 1986). If *S. morellifolium* indeed turns out to be a food source for these butterfly larvae, it may be indicative of a closer relationship of sect. *Allophylla* to *Cyphomandra* than can be inferred on the basis of morphological characters (Knapp, pers. comm.).

3. Solanum allophyllum (Miers) Standl., J. Wash. Acad. Sci. 17: 16. 1927. *Pionandra allophylla* Miers in Seem. Bot. Voy. Herald, 174. 1854. *Cyphomandra allophylla* (Miers) Hemsl., Biol. Cent.-Amer., Bot. 2: 417. 1882. TYPE: Panama: in waste places, *Seemann 169* (lectotype, BM, here designated; isolectotype, K). Figure 5.

FIGURE 5. Isolectotype of *Pionandra allophylla* (= *Solanum allophyllum*) (*Seemann 169* K).

Solanum ellipsoideibaccatum Bitter, Repert. Spec. Nov. Regni Veg. 11: 486. 1913. *Bassovia ellipsoideibaccatum* (Bitter) Pitt. Cat. Fl. Venez. 2: 356. 1947. TYPE: Colombia. Magdalena: Santa Marta, near Bonda, 150 ft., erect, branching, to 2.5 ft., rare in shady and somewhat damp places below 1,000 ft., corolla pale greenish, 12 Nov. 1898, *H. H. Smith 1153* (distributed as *Solanum chenopodioides* Lam.?) (holotype, B, destroyed; isotypes, A, BM, E, F, GH, MO, NY, P, US, VT, WIS).

Solanum ellipsoideibaccatum var. *ficilobum* Bitter, Repert. Spec. Nov. Regni Veg. 13: 173. 1914. TYPE: Panama. Chiriquí: near San Félix, 0–120 m, *Pittier 5237* (holotype, US #715441; isotype, US).

Herb or *shrub* 0.4–1.5 m tall. *Branches* glabrous or sparsely puberulent, especially when young. *Leaves* 3 per sympodial unit, the blades unlobed or pinnately 2–5-lobed, sparsely eglandular-pubescent adaxially, glabrous abaxially; if unlobed, the blade ovate, 3–14 cm long, 1.5–7.5 cm wide, the length : width ratio ca. 2 : 1; if lobed, the blade

3–14 cm long, 2–12 cm wide, the terminal lobe elliptic to obovate, 2.5–12 cm long, 1–5.5 cm wide, the lateral lobes ascending, 1–10 cm long, 0.5–4 cm wide, the blade divided nearly to midrib, the sinuses rounded, acute; major veins 4–6 on each side; petioles 1–11 cm long. *Inflorescence* extra-axillary or located in a branch fork, 4–6-flowered, 1.5–7 cm long; peduncle 1–4.5 cm long; rachis 0.5–2.5 cm long; pedicels 4–6 mm long, in fruit 6–9 mm long, spaced 3–13 mm apart. Peduncle, rachis, and pedicels glabrous, or rarely sparsely puberulent. *Calyx* glabrous, the radius 2–3 mm, the lobes deltate, acute or obtuse, apiculate, 1–2 mm long, 1.5–2 mm wide. *Corolla* white or greenish, rotate-stellate, the radius 7–10 mm, the tube 3–4 mm long, the lobes 4–6 mm long, 3 mm wide, triangular. *Stamens* 6–6.5 mm long; anther thecae yellowish or white with a greenish patch near the base, narrowly triangular, 5–6 mm long, 1.5–2 mm wide at base, ca. 0.5 mm wide at apex. *Style* 4–5 mm long, 0.3–0.5 mm diam.; stigma 0.3–0.5 mm diam. *Fruit* ovoid or ellipsoidal, laterally compressed, 2.5–4 cm long, 1.5–2.5 cm wide, 1–1.8 cm thick, white or light yellow to orange, often with dark green or purple stripes; mesocarp with 3–6 stone cell aggregates ca. 2 mm diam.; seeds 2 mm long, 1.5 mm wide, rugose-verrucate.

Distribution. Forest and disturbed areas, especially in drier sites, Honduras to Panama, Colombia, and Venezuela, 0–900 m (Fig. 3). All collections from Panama are from Tropical Moist Forest, sensu Holdridge et al. (1971).

Flowering and fruiting. April through January.

Vernacular names. Bleo de gallinazo (*Romero 6321*) (probably a misprint for *bledo*, a Spanish term for herbs that can be used as food (Hunziker, pers. comm.), *cumapan* (*Delascio & Liesner 6988*), *hierba de gallinazo* (*Standley 28138*), *hierba gallota* (*Pittier 6788*), *yerba de gallote* (*Bro. Paul 154*), *zopilote* (*Moreno 22030, Nee 28133*).

Uses. Leaves used in salads, broths, and chopped meat dishes; ripe fruits used in stews (Colombia, from Romero-Castañeda, 1965).

Additional specimens examined. HONDURAS. CHOLUTECA: vicinity of Pespire, 160–200 m, 18–25 Oct. 1950, *Standley 27108* (BM, F, US); same locality, 18–27 Oct. 1950, *Standley 27237* (F). NICARAGUA. BOACO: Monte Grande, 12°25′N, 85°45′W, 200 m, 30 Sep. 1980, *Moreno 3286* (MO); San Lorenzo, Sierra El Espino, 12°23′N, 85°39′W, 500–600 m, 11 Nov. 1982, *Moreno 18544* (MO); Santa Cruz, 12°24′N, 85°49′W, 160–200 m, 15 Nov. 1982, *Moreno 18608* (MO). CHONTALES: La Asunción, km 120 carretera Juigalpa, 12°9′N, 85°31′W, 120 m, 19 Oct. 1980, *Moreno 3705* (MO); Hda. San Martín, near confluence of Río El Jordan and Río La Pradera, 12°17′N, 85°15′W, ca. 390 m, 30 July 1984, *Stevens 22977* (MO, NY). GRANADA: Laguna de Apoyo, "Babilonia," 11°55′N, 86°4′W, ca. 40–80 m, 30 May 1981, *Moreno & Henrich 8898* (MO); camino de Casa Tejas, 11°46′N, 85°54′W, ca. 40–60 m, 21 June 1982, *Moreno 16658* (MO). LEÓN: Isla de Momotombito, Lago de Managua, ca. 200 m, 21 Oct. 1979, *Araquistain 362* (MO); same locality, ca. 150 m, 22 Oct. 1979, *Araquistain 386* (MO). MANAGUA: El Carrizo, carretera a San Francisco, 12°23′N, 86°7′W, ca. 70–80 m, 10 Dec. 1980, *Moreno 5080* (MO). MASAYA: Laguna de Apoyo, 11°56′N, 86°2′W, 100–140 m, 20 Sep. 1981, *Moreno 11149* (MO). MATAGALPA: carretera a Jinotega, km 134, 800–900 m, July 1982, *Bustos 44* (HNMN). RIVAS: Isla de Ometepe, 11°29′N, 85°29′W, 40–55 m, 14 Sep. 1983, *Moreno 22030* (MO); above Balgue on facing slopes of Volcán Maderas, Isla de Ometepe, 11°28′N, 85°31′W, 600 m, 14 Sep. 1983, *Nee & Téllez 28019* (MO, NY); same locality, 11°29′N, 83°31′W, 50–100 m, 15 Sep. 1983, *Nee 28133* (MO, NY); Isla de Ometepe, Volcán Maderas, "La Palma," 11°27–29′N, 85°28–30′W, 100–200 m, 21 Sep. 1984, *Robleto 1221* (MO); Isla de Ometepe, entre Cuatro Esquinas y San Fernando, 11°30–32′N, 85°33–34′W, 17 July 1981, *Sandino 1017* (MO). COSTA RICA. GUANACASTE: La Pacifica, Nov. 1976, *Haber 57* (F, MO); between Las Cañas and Liberia, Pan American Highway, 100 ft., 12 Nov. 1953, *Heiser 3719* (US); Santa Rosa National Park, 25 Sep. 1975, *Janzen 10221* (MO); same locality, ca. 10°50′N, 85°37′W, 0–320 m, 1 July 1981, *Janzen 12083* (MO); along Río Higuerón near agricultural experimentation area near Taboga, 10°20′N, 85°12′W, 0–100 m, 29–30 June 1977, *Liesner et al. 2724* (MO); Finca La Pacifica, Cañas, Central Farm Road, 22 Oct. 1971, *Opler 472* (MO). PANAMA. CANAL ZONE: Barro Colorado Island, 1931, *Aviles 105* (F); vicinity Cerro Viejo on K16C, 13 Oct. 1965, *Blum 1263* (MO); Farfan Beach, from Thatcher Hwy. to Palo Seco, 27 Dec. 1966, *Burch et al. 1410* (MO, NY); Gatún, Nov. 1859, *Hayes 563* (NY); vicinity of Madden Dam, 50 ft., 3 Dec. 1966, *Lewis et al. 27* (M, MO); Madden Forest Preserve, along Las Cruces Trail and highway, 8 Apr. 1969, *Lewis et al. 5315* (MO); Sosa Hill, Balboa, 27 Nov.–10 Dec. 1923, *Standley 25289* (US); Balboa, Nov. 1923–Jan. 1924, *Standley 25449* (US), *26109* (US); vicinity of Summit, 7 Jan. 1924, *Standley 30142* (US); Barro Colorado Island, El Cermeño, 1 Dec. 1942, *Zetek 5040* (F, MO). COLÓN: along Quebrada Bonita, 3 km NW of Salamanca, 13 km NE of Buena Vista, 150 m, 15 Sep. 1973, *Nee 6970* (C, MO). DARIÉN: near mouth of Río Yapé, ca. 20 m, 12–14 July 1937, *P. H. Allen 326* (F, MO); vicinity of Pinogana, ca. 20 m, 6 Oct. 1938, *P. H. Allen 939* (F, MO, NY, US). PANAMÁ: Bayano, 24 Nov. 1973, *Alvarado 42* (F); Cerro Campana, 12 Nov. 1975, *D'Arcy 9613* (MO); ca. 6 mi. E of Chepo on Pan Am Highway, 28 Sep. 1961, *Duke 4091* (MO); same locality and date, *Duke 4092* (MO); vicinity of El Llano, 14–19 Oct. 1962, *Duke 5798* (MO); Tumba Muerto antes del puente que queda cerca del Cicle Club, 24 Oct. 1974, *Garrido 30* (MO); Natural Bridge, near Madden Lake, 3 Aug. 1972, *Gentry 5604* (AAU, MO); Camino de Las Sabanas, 28 Nov. 1921, *Bro. Heriberto 256* (US); Juan Díaz, 10 Nov. 1973, *Herrera 42*

(MO); same locality, 25 m, 30 Sep. 1917, *Killip 3100* (MO); along Tapia River, 75 m, 21 Oct. 1917, *Killip 3154* (MO); 1 km S of Madden Dam, 80 m, 20 Dec. 1973, *Nee 8900* (F—photos, MO), *8901* (MO); Sabanas, NE of Panama City, Oct. 1932, *Bro. Paul 154* (US); same locality, Nov. 1932, *Bro. Paul 175* (GH); Chepo, 60 m, Oct. 1911, *Pittier 4689* (BM, US); agricultural experiment station at Matías Hernández, 10 Sep. 1914, *Pittier 6788* (US); Taboga Island, Dec. 1923, *Standley 27089* (BM, US); Río Tapia, 7 Dec. 1923–11 Jan. 1924, *Standley 28138* (US); Río Tecumen, 3 Jan. 1924, *Standley 29461* (US). SAN BLAS: on mainland in front of Ustupo, 9 Nov. 1975, *D'Arcy 9472* (MO); cult. at Missouri Bot. Gard. from seed of *D'Arcy 9472*, 1976, *D'Arcy 9472a* (MO); on mainland in front of Ustupo, 9 Nov. 1975, *D'Arcy 9529* (MO, NY); Ailigandi area along trail from ocean to waterfall on river, 0–200 m, 7 Oct. 1978, *Hammel & D'Arcy 5002* (MO). COLOMBIA. BOLÍVAR: La Popa, near Cartagena, 50–175 m, 2 Nov. 1926, *Killip & Smith 14080* (GH, NY, US); Torrecilla, near Turbaco, 150–300 m, 7–19 Nov. 1926, *Killip & Smith 14647* (F, NY). CESAR: Rincón Hondo, 11 Aug. 1924, *C. Allen 373* (MO); same locality, 18 Aug. 1924, *C. Allen 423* (MO); same locality, 20 Aug. 1924, *C. Allen 451* (MO); Poponte, 23 Sep. 1924, *C. Allen 737* (MO); Becerril, ca. 100 m, 15 Sep. 1943, *Haught 3674* (US). CHOCÓ: alrededores de Tilupo, 21 June 1957, *Romero 6321* (F, MO, NY). GUAJIRA: Cerrejón, ca. 200 m, 3 Oct. 1949, *Haught 6637* (US). NORTE DE SANTANDER: valle del Río Peralonso en los alrededores de Santiago, 120 m, 21 Dec. 1948, *Molina & Barkley 86* (MO, US). SANTANDER: Barranca Bermeja, Magdalena Valley, between Sogamoso and Carare rivers, on Aguas Blancas Creek ca. 25 km S of El Centro, 150 m, 20 Nov. 1936, *Haught 2084* (F, GH). VENEZUELA. BOLÍVAR: Dist. Piar, La Camilera, 40 km al W de El Manteco, 250–260 m, July 1978, *Delascio & Liesner 6988* (MO, NY). GUÁRICO: ca. 39 km SSW of Calabozo on Hato Masaguaral, 100 m, 8°56′N, 67°60′W, 9 Nov. 1982, *Rondeau 123* (US). ZULIA: Dtto. Bolívar, vía entre la carretera Lara–Zulia y Piedras Blancas (desviando en km 70 de la Lara–Zulia al SE del puente sobre el lago), entre km 1–3, 24 May 1979, *Bunting & Fucci 7651* (MO); San Martín, on Río del Palmar, Urdeneta, 15 Oct. 1922, *Pittier 10530* (US); vicinity of Mene Grande, 31 Oct. 1922, *Pittier 10610* (GH, NY, US).

Solanum allophyllum differs from the other species of the section by its large, ellipsoidal fruits and frequently pinnately lobed leaves. The unlobed leaves are very similar in size and shape to those of *S. morellifolium*. The flowers of *S. allophyllum*, though rather large like those of *S. mapiriense*, are rotate-stellate with short lobes like those of *S. morellifolium*. Details of the architecture, branching pattern, compatibility, and cytology of *S. allophyllum* may be found in Bohs (1989).

The herbarium sheet of *Seemann 169* at the British Museum (BM) bearing Miers's annotation has been chosen as the lectotype of *Pionandra allophylla* Miers.

Two collections are included here that show morphological features more characteristic of *S. morellifolium* than of *S. allophyllum*. I have identified them as *S. allophyllum* because of their occurrence in northwestern South America (Fig. 3). Haught's collection *2084* bears only flowers. The vegetative features conform to those of *S. allophyllum*, but the inflorescence is axillary, few-flowered, and has very small flowers, all characteristics more typical of *S. morellifolium* than of *S. allophyllum*. The collection *Rondeau 123* also resembles *S. allophyllum* in vegetative features, except for denser puberulence than is usual in that species. The fruits on this collection are globose and less than 1 cm in diameter. Although it is not known if these fruits are mature, their size and shape are more typical of *S. morellifolium* than of *S. allophyllum*. No flowers are present on this collection.

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NOTES

TWO NEW SPECIES AND A NEW COMBINATION IN *VISMIA* (GUTTIFERAE–HYPERICOIDEAE)

Work on the Guttiferae subfamily Hypericoideae for the *Flora of the Venezuelan Guayana* has revealed three species of *Hypericum* and 14 species of *Vismia* in the area of the *Flora*. Two of the *Vismia* species, one widespread and the other endemic, are new and are described below. Another was previously recognized as a variety and is here elevated to specific status.

Vismia schultesii N. Robson, sp. nov. TYPE: Colombia. Amazonas–Vaupés: Río Apaporis, Raudal Jirijirimo (below mouth of Kananarí), 0°05′N, 70°40′W, ca. 270 m, 21 Jan. 1952, *Schultes & Cabrera 14946* (holotype, BM; isotypes, NY, U).

Arbor 3–13.5 m alta, latice rubro ramulis dense fusco-chocolatino-tomentellis. Folia petiolo 10–20 mm longo; lamina (100–)140–280 × 50–145 mm, late ovata vel ovato-oblonga vel oblonga vel rare lanceolata, apice apiculata vel breviter acuminata, basi profunde cordata vel rotundata vel raro late cuneata, venis lateralibus principalibus 13–17 jugis, venis lateralibus subsidiariis plerumque nullis, coriacea, supra atrovirens, infra ferrugineo-tomentella, haud glabrescens. Inflorescentiae terminales et interdum e nodis duobus superioribus ortae, rotundato-pyramidales, ramulis dense fusco-chocolatino- vel ferrugineo-tomentellis, alabastris globosis vel late ovoideis. Flores homostyli; sepala 6–8 mm longa, inaequalia vel subaequalia exteriora elliptico-oblonga vel omnia anguste oblonga, paginis in alabastro expositis dense adpresso-fusco-chocolatino- vel ferrugineo-tomentellis, marginibus in alabastro obtectis saltem distaliter ciliatis, sub fructu patula; petala alba vel flava, rufo-glanduloso-lineata vel distaliter -punctata, 8 10 mm longa, obovata; staminorum fasciculi decidui; ovarium subglabrum stylis hirsutis. Fructus immaturus virens, 10 mm longus, ovoideo-globosus, haud vel sparsissime glanduloso-punctatus.

Tree 3–13.5 m tall, latex red, young branches densely dark-chocolate-tomentellous. Leaves with petiole 10–20 mm long; lamina (100–)140–280 × 50–145 mm, broadly ovate or ovate-oblong to oblong or rarely lanceolate, apex apiculate to shortly acuminate, base deeply cordate to rounded (or rarely broadly cuneate), main lateral veins 13–17 pairs, subsidiary laterals usually absent, coriaceous, dark green above, ferrugineous-tomentellous beneath, not glabrescent. Inflorescences terminal and sometimes axillary, rounded pyramidal, axes densely dark-chocolate- to ferrugineous-tomentellous, buds globose to broadly ovoid. Flowers homostylous; sepals 6–8 mm long, unequal or subequal, outer elliptic-oblong or all narrowly oblong, exposed surfaces (in bud) densely appressed-dark-chocolate- to ferrugineous-tomentellous, inner margins at least distally ciliate, spreading in fruit; petals white to yellow with glands linear, reddish, 8–10 mm long, obovate; stamen fascicles deciduous; ovary subglabrous. Fruits (immature) green, 10 mm long, ovoid-globose, not or very sparsely gland-dotted.

Vismia schultesii is a lowland species of gallery forest and white sand forest and savanna in the extreme south of Venezuela and elsewhere in the Amazonian basin from Pará to Rondônia (Brazil), southern Colombia, Peru (Loreto), and adjacent Ecuador.

Additional specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Río Negro, Río Siapa entre su boca y la boca del Río Emoni, 16–18 Apr. 1985, *Stergios, Aymard & Nico 8275* (BM, MO, PORT). COLOMBIA. GUAINÍA: 1°47′N, 67°06′W, 6 Apr. 1984, *Gentry & Stein 46392* (BM, MO). VICHADA: Parque Nacional Natural "El Tuparro," ca. 20 km NNE of El Tapór, 5°13′N, 69°05′W, 20 Mar. 1985, *Zarucchi & Barbosa 3792* (BM, MO). VAUPÉS: Mitu, 22 Oct. 1976, *Davis 110* (U). AMAZONAS-VAUPÉS: Río Apoporis, entre los ríos Kananarí y Pacoa, 250 m, 21 Jan. 1951, *Schultes & Cabrera 12728* (NY, U); Río Apaporis, Soratama, 1–15 Dec. 1951, *Garcia-Barriga 14046* (NY). AMAZONAS: 18–22 km N of Leticía, near Los Alpes, 19 Nov. 1974, *Gentry 12762* (BM, MO); Leticía and vicinity, 21 Jan. 1968, *Stout 20* (NY). PUTUMAYO: Mocoa, Pueblo Viejo, 580–600 m, 28 Dec. 1940, *Cuatrecasas 11385* (F, US). ECUADOR. PASTAZA: Río Curaray, 1°40–41′S, 75°55–48′W, 200 m, 4 June 1980, *Brandbyge & Asanza 31497* (AAU, BM). PERU. LORETO: Río Putomayo at mouth of Río Yubineto, Florida, ca. 180 m, May–June 1931, *Klug 2263* (BM, F, K, NY); upper Río Nanay, Timbuchí, 26 June 1929, *Williams 9676* (F), upper Río Nanay, Manfinfa, 30 June 1929, *Williams 1144*, (F);

Iquitos, San Roque, 17 Oct. 1973, *Ayala 468* (BM, MO). BRAZIL. AMAZONAS: Rio Solimões, mun. São Paulo de Olivença, creek Belem, 26 Oct.–11 Dec. 1936, *Krukoff 8728* (BM, K, F, NY, P, U); Manaus area and lower Rio Negro, *Chagas 5887* (NY), *Chagas MG 21209* (NY), *Ducke 206* (F, K, NY), *Jaccoud 89* (NY), *Lowe 4235* (E), *Luiz MG 21193* (NY), *Maas & Maas 219A* (K, NY, U), *Prance et al. 2215* (BM, NY), *4988* (NY), *5553* (NY), *9535* (BM, NY), *11528* (NY), *Riedel 1427* (NY), *da Silva 4508* (BM, NY); Rio Purús, Coa, 31 Jan. 1955, *Ferreira 33-55* (NY). RONDÔNIA: basin of Rio Madeira, Abuña, 18 Nov. 1968, *Prance et al. 8593* (NY); basin of Rio Madeira, Mutumparaná, 5 July 1968, *Prance et al. 5553* (BM, K, NY); Porto Velho–Cuiabá highway, Santa Barbara, 12 Aug. 1968, *Prance & Ramos 6896* (BM, NY); Porto Velho–Cuiabá highway, near Ariquemes, 17 Aug. 1968, *Forero & Wrigley 7136* (BM, NY). PARÁ: Santarém, Palhao to Igarape do Pilao road, 18 Aug. 1969, *Silva & Sousa 2311* (BM, NY).

Vismia schultesii is closely related to the widespread Amazonian *V. japurensis* Reichardt but differs in having leaves usually broadly ovate to oblong rather than broadly ovate to lanceolate with the base sometimes more deeply cordate and the lower surface ferrugineous, not tawny to mustard-brown; sepals shorter, chocolate-tomentellous, the outer ones elliptic-oblong to narrowly oblong, not ovate; petals shorter.

Some specimens of *V. schultesii* have been identified by Ewan as *V. tomentosa* Ruiz & Pavon and *V. catachrysa* sp. ined.

Vismia steyermarkii N. Robson, sp. nov. TYPE: Venezuela. Bolívar: alto Río Cuyuni, Río Uiriyuk, La Escalera, 500–600 m, 20 Aug. 1962, *B. & C. Maguire & Steyermark 46799* (holotype, BM; isotype, NY).

Arbor 3–5 m alta, colore laticis ignota, ramulis dense chocolatino-tomentellis. Folia petiolo 8–15 mm longo; lamina (95–)110–180 × (35–)40–65 mm, elliptica vel rarius elliptico-lanceolata, apice apiculata vel breviter acuminata, basi rotundata vel cuneata, venis lateralibus principalibus 10–14 jugis, venis lateralibus subsidiariis plerumque nullis, subcoriacea, supra atrovirens, infra castaneo- vel cinnamomeo-tomentella, haud glabrescens. Inflorescentia terminalis, breviter rotundato-pyramidalis, ramulis dense adpresso-fusco-chocolatino-tomentellis, alabastris late ellipsoideis. Flores verosimiliter heterostyli; sepala 5–7 mm longa, subaequalia, anguste oblonga vel lanceolata, paginis in alabastro expositis dense adpresso-chocolatino-tomentellis, marginibus in alabastro obtectis ciliatis, sub fructu patula; petala albido-virentia vel eburnea, sparse glanduloso-punctata, 7–8(–9?) mm longa, oblanceolata; staminorum fasciculi demum decidui; ovarium glabra, stylis glabris. Fructus immaturus virens, 8 mm longus, globosus, brunneo-glanduloso-punctatus.

Tree 3–5 m tall, latex color unknown, young branches densely chocolate-tomentellous. Leaves with petiole 8–15 mm long; lamina (95–)110–180 × (35–)40–65 mm, elliptic or more rarely elliptic-lanceolate, apex apiculate to shortly acuminate, base rounded to cuneate, main lateral veins 10–14 pairs, subsidiary laterals usually absent, subcoriaceous, dark green above, chestnut- to cinnamon-tomentellous beneath, not glabrescent. Inflorescence terminal, shortly rounded-pyramidal, axes densely appressed-chocolate-tomentellous, buds broadly ellipsoid. Flowers probably heterostylous; sepals 5–7 mm long, subequal, narrowly oblong to lanceolate, exposed surfaces (in bud) densely appressed-tomentellous, inner margins ciliate, spreading in fruit; petals greenish white to cream with glands sparsely punctiform, 7–8(–9?) mm long, oblanceolate; stamen fascicles eventually deciduous (?); ovary glabrous. Fruits (immature) green, 8 mm long, globose, brown-gland-dotted.

Vismia steyermarkii, a species of montane woodland at 500–1,040(–1,300?) m, is known only from southeastern Venezuela, from the upper Río Cuyuni south of El Dorado into La Gran Sabana.

Additional specimens examined. VENEZUELA. BOLÍVAR: Cerro La Danta, NW of Cerro Venamo, headwaters of Río Venamo, 1,040–1,060 m, 13 Apr. 1960, *Steyermark & Nilsson 17* (NY); Roraima Plateau, Río Cuyuni 132.5 km S of El Dorado, 865–1,300 m, 26–27 July 1970, *Steyermark & Dunsterville 104494* (NY); Santa Elena–El Dorado road on Gran Sabana, 114 km N of Santa Elena, 1,040 m, 27 July 1982, *Croat 54313* (BM, MO); Carretera El Dorado–Santa Elena de Uairén, km 107, 560 m, 13 Aug. 1957, *Trujillo 3517* (MY, U).

Vismia steyermarkii appears to be a higher-altitude relative to *V. schultesii*, differing from it usually in stature and in having smaller, usually elliptic leaves with a narrower base, chestnut- to cinnamon-colored (not ferrugineous) beneath; flower buds broadly ellipsoid; flowers probably heterostylous, the petals greenish white to cream, shorter, and with glands punctate only; glabrous styles; and (immature) fruits smaller and gland-dotted.

Vismia tenuinervia (E. v.d. Berg) N. Robson, comb. et stat. nov. *Vismia cayennensis* var. *tenuinervia* E. v.d. Berg, Acta Amazonica 4: 16, f. 19. 1974.

I am grateful for the loan of material of *Vismia* to the curators of DUKE, F, MO, NY, and U.

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DOS ESPECIES NUEVAS DEL GENERO *SCHWENCKIA* (SOLANACEAE) DE VENEZUELA

Durante un estudio sobre la tribu Schwenckieae (Solanaceae) para la flora de Venezuela, he encontrado dos nuevas especies del género *Schwenckia*: *S. huberi* Benítez, del Territorio Federal Amazonas, Departamento Atures, y *S. trujilloi* Benítez, del Parque Nacional Henri Pittier, Estado Aragua. La primera pertenece a la sección *Schwenckia* y la segunda a la sección *Cestranthus* Benth.

Schwenckia huberi Benítez, sp. nov. TIPO: Venezuela. Territorio Federal Amazonas: Depto. Atures, en sabanas arenosas al noreste de Galipero, vía Puerto Ayacucho ca. 80 m, 27 Feb. 1986, *C. E. Benítez de Rojas & F. Rojas 3397* (holotipo, MY; isotipos, MO, MYF, NY, VEN). Figuras 1, 2.

Herba repens radice axonomorpha instructa, caule primario brevissimo in ramos elongatos repentesque argenteo-virides, dense villoso-sericeos, pilis erectis praeditos, subdiviso. *Folia* firme papyracea, petiolis 3–6 mm longis villoso-sericeis, pilis erectis; lamina elliptica late ovata, interdum late ovata, (10–)13–20(–40) mm longa, (4–)6–13 mm lata, utrinque villoso-sericea, pilis elongatis rectis, vulgo erectis, apice obtusa vel acuta, basi cuneata vel late cuneata, nervis primariis conspicuis, tribus venarum paribus auctis. *Inflorescentia* terminalis, erecta, usque ad 55 cm alta, laxe paniculata, nuda, axe glabro, rubescenti-nitido. *Flores* plurimi, sed plerumque decidui, pauci fructificantes; pedicellis 2–4 mm longis, glabris. *Calyx* tubulosus 4 mm longus, extus laxe pilosus, 5-lobulatus, lobulis acutis 1 mm longis. *Corolla* recta, glabra, obscura, violaceo vel badio suffusa, 1.1–1.2 cm longa, 5 lobulis mediis claviformibus minus 1 mm longis lobulis lateralibus contiguis coalitis inter utrunque emarginatis, papillosis, lobulos medios non attingentibus. *Stamina* fertilia duo, filamentis laminaribus, basim versus pubescentibus, antheris 1 mm longis. *Fructus* calyce incluso, globosus 2–2.5 mm diam., seminibus 10–20, obscure castaneis.

Hierba rastrera, de raíz axonomorfa, tallo principal muy corto ramificándose en largas ramas rastreras, éstas plateado-verdosas y densamente velloso-seríceas, los pelos erectos. Hojas firme-papiráceas, con pecíolos 3–6 mm largo, velloso-seríceos, con pelos erectos; lámina elíptica u ovada, a veces angosto elíptica o angosto ovada o más frecuentemente ancho ovada, (10–)13–20(–40) mm largo y (4–)6–13 mm ancho, velloso sericea en la haz y en el envés, los pelos largos, erectos y en ambas caras entremezclados; ápice obtuso o agudo, base cuneada o ancho cuneada, la nervadura principal sobresaliente con 3–5 pares de venas secundarias. Inflorescencia terminal, erguida, hasta 55 cm alto, en panícula muy laxa, desnuda, con eje glabro, rojizo y lustroso. Flores muchas, en general caedizas, fructificando pocas; pedicelos 2–4 mm largo, glabros. Cáliz tubular 4 mm largo, laxo-piloso por fuera, 5-lobulado, lóbulos agudos, 1 mm largo. Corola erecta, glabra, oscura con tonos violáceos o castaños, 1.1–1.2 cm largo, con 5 lóbulos medios claviformes menores de 1 mm de largo, lóbulos laterales contíguos unidos formando entre sí emarginadura, papilosos, más cortos que los lóbulos medios. Estambres fértiles 2, filamentos laminares, hacia la base pubescentes, anteras 1 mm largo, oblongas. Fruto parcialmente incluído en el cáliz, globoso 2–2.5 mm diám.; semillas 10–20, de color castaño oscuro.

Habitat y distribución. En sabanas arbustivas sobre suelo bien drenado, localizada en el Territorio Federal Amazonas, Departamento Atures, Venezuela.

Esta especie es dedicada al Dr. Otto Huber, biólogo especialista en ecología tropical, quien ha contribuído al conocimiento de la flora y vegetación de la Guayana venezolana, con sus fecundas exploraciones botánicas.

Paratipos. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Depto. Atures: sabanas y bosques en la región de Rincones de Chacorro, unos 30 km al N de Puerto Ayacucho y a unos 5 km al NE de Galipero, 5°48′N, 67°20′W, ± 80 m, 4 Nov. 1980 (fr), *Otto Huber 5736* (MY, VEN); 27 Feb. 1982 (fr), *6280* (MY, VEN); 7 Nov. 1979 (fl), *4650* (VEN); 18 June 1980 (fl), *5264* (VEN); bastante frecuente en sabana arenosa en Rincones de Chacorro, al N de Puerto Ayacucho, entre Galipero y Pozo Azul, 30 abr. 1988 (fl, fr), *Benítez de Rojas et al. 3959* (F, K, MO, MY, PORT, TFAV, VEN).

Schwenckia huberi, perteneciente a la sección *Schwenckia*, es muy peculiar por el indumento velloso-seríceo, tanto en los tallos como en las hojas. Su hábito de crecimiento rastrero con ramas largas, plateado-verdosas y sus hojas firme papiráceas, la diferencian de *S. americana*, su especie más relacionada. De *S. elegans* difiere porque en esta última, las hojas son fasciculadas y con el margen ligeramente ondeado.

FIGURA 1. *Schwenckia huberi* (*Benítez de Rojas et al. 3959* MY).—Habito.

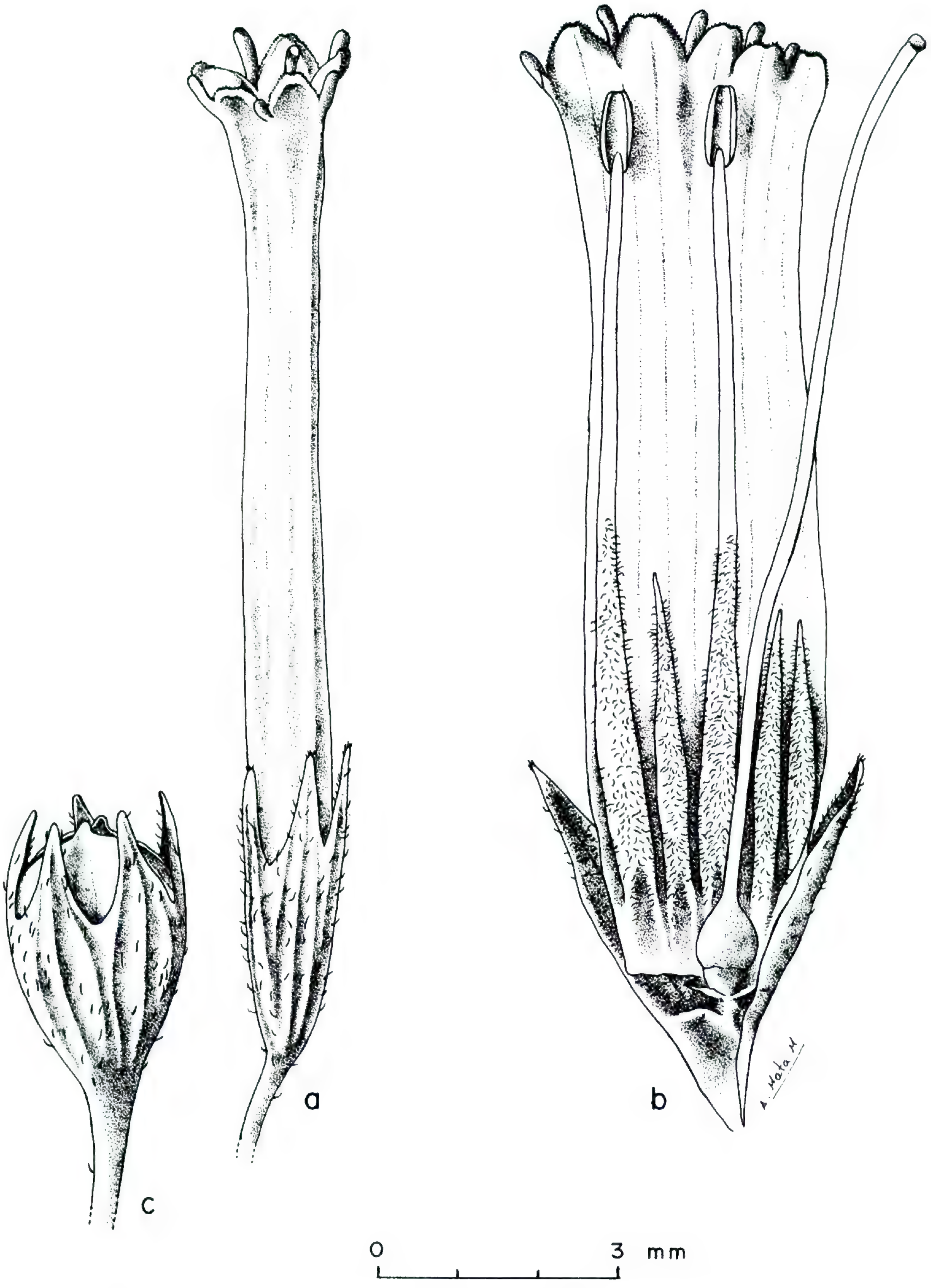

FIGURA 2. *Schwenckia huberi* (*Huber 5736* MY).—a. Cáliz y corola.—b. Vista interna de la corola expandida.—c. Fruto.

FIGURA 3. *Schwenckia trujilloi* (*C. Benítez de Rojas, F. Rojas & V. Badillo 3839* MY). Rama mostrando hojas e inflorescencia.

Schwenckia trujilloi Benitez, sp. nov. TIPO: Venezuela. Aragua: Dtto. Girardot, en barrancas de la carretera a Guamitas, Parque Nacional Henri Pittier ± 700 m, 17 Ag. 1963, *Baltasar Trujillo 5745* (holotipo, MY; isotipo, VEN). Figuras 3, 4.

Frutex pluricaulis, caulibus badio-olivaceis, 2–3 mm diam., usque 4 m longis, primum erectis et aphyllis, dein flexuosis paulo ramosis ac foliosis. *Folia* membranacea, petiolis 9–25 mm longis pubescentibus; pagina late ovata, 3–7 cm longa, 1.5–4 cm lata, supra pilis ascendentibus conspersa, subtus pilis praesertim secus nervos, apice attenuata vel acuta, basi late subcordata vel cordata.

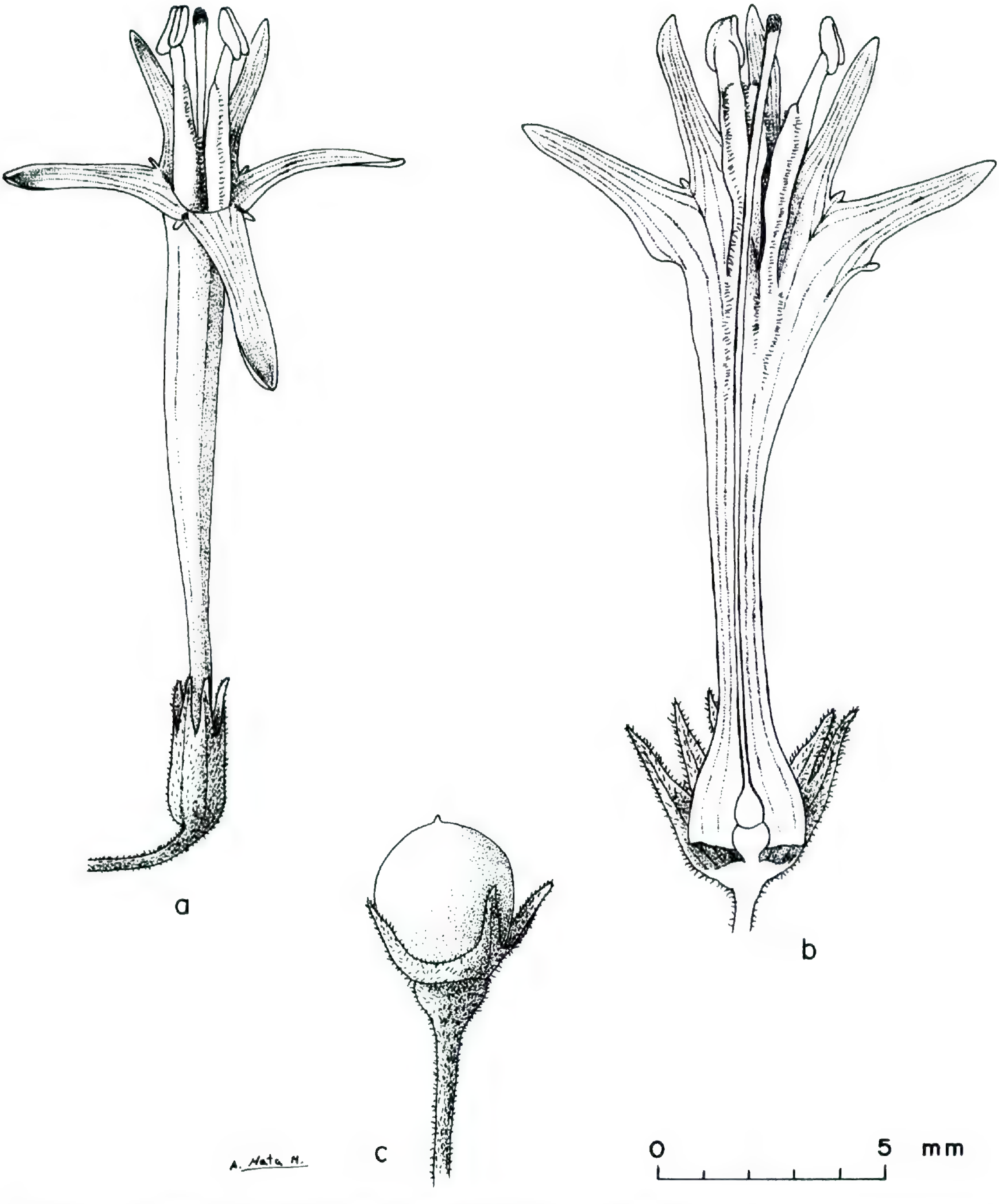

FIGURA 4. *Schwenckia trujilloi* (*Baltasar Trujillo 5745* MY).—a. Vista de frente de flor abierta en su extremo superior.—b. Sección longitudinal de la misma.—c. Fruto.

Inflorescentiae paniculatae axillares vel terminales, laxae, expansae; pedicellis 3–6 mm longis pilosis. *Calyx* tubulosus 3–3.5 mm longus, extus intusque pilosus, 5-lobulatus, lobulis 1–1.5 mm longis. *Corolla* erecta, glabra, viridi-violacea, 1.5 2 cm longa, tubo cylindraceo, superius sensim ampliatus, 5 lobulis mediis dentiformibus recurvatis minimis praedito, lobulis lateralibus contiguis coalitis ± triangularibus, pilis brevibus marginatis 3–4 mm longis. *Stamina* fertilia duo, exserta; filamentis parte superiori laminatis pubescentibusque, antheris 1 mm longis, oblongis, extrorsis. *Stylus* exsertus. *Fructus* globosus, 3–3.5 mm diam., calyce sub lobulos constricto; seminibus 6–14, obscure castaneis rubescentibus.

Arbusto hasta 4 m largo, de varios tallos de 2–3 mm diám., marrón oliváceo, partiendo de una base leñosa común, al comienzo erguidos y sin

hojas, luego flexuosos poco ramificados y foliosos, con pelos antrorsos especialmente en los tallos jóvenes. Hojas membranáceas, con pecíolos 9–25 mm largo, pubescentes; lámina ancho-ovada, 3–7 cm largo y 1.5–4 cm ancho, haz con pelos esparcidos, ascendentes, envés con pelos especialmente en las nervaduras, ápice atenuado o agudo, base ancho subcordada o cordada. Inflorescencia en panícula axilar o terminal, laxa; pedicelos 3–6 mm largo, pilosos, Cáliz tubular 3–3.5 mm largo, piloso por fuera y dentro, 5-lobulado, lóbulos 1–1.5 mm largo. Corola erecta, glabra, verde violácea, 1.5–2 cm largo, tubo cilíndrico, con la parte superior un tanto ensanchada, con 5 lóbulos medios dentiformes, curvos, mínimos, lóbulos laterales contíguos unidos formando una porción ± triangular, glabros, 3–4 mm largo. Estambres fértiles 2, exsertos; filamentos laminares en su parte superior, allí pubescentes, anteras 1 mm largo, oblongas, extrorsas. Estilo exserto. Fruto globoso 3–3.5 mm diám., con el cáliz constricto abajo de los lóbulos; semillas 6–14, de color castaño oscuro o rojizo.

Habitat y distribución. Crece en arbustales sobre taludes, en suelos deleznables, localizada sólo en el Parque Nacional Henri Pittier, Estado Aragua, Venezuela.

Dedicamos esta especie al destacado botánico Profesor Baltasar Trujillo, quien hizo especiales observaciones de campo a la muestra que se ha escogido como holotipo.

Paratipos. VENEZUELA. ARAGUA: Parque Nacional Henri Pittier, 2 km después de la alcabala, subiendo por la carretera hacia Ocumare de la Costa, creciendo en el talud, 600 m, 10 dic. 1987 (fl, fr), *Benítez de Rojas & F. Rojas 3756* (MY, PORT, US, VEN); 29 dic. 1987 (fl), *Benítez de Rojas et al. 3838* (MY); 29 dic. 1987 (fl, fr), *C. Benítez de Rojas, F. Rojas & V. Badillo 3839* (F, MO, MY, NY, P, US).

Esta especie, de la sección *Cestranthus*, muestra afinidad con *S. grandiflora* Benth., diferenciándose por ser una planta perenne de tallos alargados hasta 4 m de largo, flexuosos pero no trepadores; con hojas menores de 7 cm de largo y de 4 cm de ancho, siendo las hojas de *S. grandiflora* Benth. mayores de 7 cm de largo y de 4 cm de ancho. Las flores miden hasta 2 cm de largo en *S. trujilloi* Benítez y más de 2 cm en *S. grandiflora* Benth.

La autora agradece a Bruno Manara, quien elaboró la descripción latina de las especies y a Arístides Mata, quien realizó las Figuras.

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A NEW SPECIES OF *TRIGONOSPERMUM* (COMPOSITAE, HELIANTHEAE) FROM CENTRAL AMERICA

In preparing treatments of Compositae for the *Flora de Nicaragua* project, an unusual specimen was discovered in the genus *Trigonospermum* that could not be placed with existing revisionary literature (McVaugh & Laskowski, 1972; Turner, 1978). Examination of material of the genus from other institutions revealed additional specimens and led us to treat these as a new taxon at the specific level.

Trigonospermum stevensii Sundberg et Stuessy, sp. nov. TYPE: Nicaragua. Depto. Madriz: Cerro Quisuca, lower S and SW slopes, ca. 13°30′N, 86°31′W, 800–1,100 m, dry forest on rocky slopes, 23 Nov. 1979, *W. D. Stevens & A. Grijalva 16156* (holotype, OS; isotypes, MO, OS, OSH). Figure 1.

A *T. annuo* McVaugh & Laskowski et *T. melampodioide* DC. simile, sed paleis exteriores glabris, apice ciliatis, floribus radii 3–4, ramis styli 0.9–1.4 mm longis, ligulis 4.5–7 mm longis, achaeniis 2.5–3.2 mm longis, floribus disci 18–25, lobis corollae sparsim pubescentibus vel glabris, antheris 1.1–1.3 mm longis.

Annual herb, ca. 1 m tall. Stems hispidulous, stalked-glandular. Leaves opposite; blades rhombic-ovate, 5–15.5 cm long and 3–11 cm wide, hispidulous and occasionally glandular above, strigose and glandular below, acute at the apex, with margin serrulate; petiole winged, to 5.5 mm long. Peduncle slender, hispid, stalked-glandular. Capitula numerous; involucre 2.8–4 mm tall; outer phyllaries linear-elliptic, 2.4–4 mm long, 0.8–1.6 mm wide, hirtellous, glandular, grading into middle phyllaries; middle phyllaries rhombic to obovate, slightly keeled, 2.2–3.2 mm long, apex acute to apiculate, fimbriate-ciliate; inner phyllaries wrapping around achenes, obovate, scarious, white, 2.2–3 mm long, 10-nerved, glabrous except at the rounded, fimbriate-ciliate apex. Ray florets 3–4; corollas yellow; ligules 4.5–7 mm long, 3–6 mm wide, gland-dotted both sides, deeply trilobed, with lobes rounded, 2–4 mm long; tube pubescent, 0.3–0.5 mm long; style branches 0.5–1.4 mm long; achenes broadly elliptic to obovate, sometimes 3-angled, broadest above the middle, 2.5–3.2 mm long, with terminal scar elevated 0.2 mm. Disk florets 18–25, with abortive ovaries; corollas 2.1–2.7 mm long; lobes 5, 0.1–0.3 mm long, glabrous to sparsely pubescent; styles fused (not bifid); anthers 1.1–1.3 mm long, exserted half their length at anthesis. Pales filiform-subulate to oblanceolate, fimbriate at apex, 1.8–2.6 mm long.

Additional specimens examined. GUATEMALA. DEPTO. CHIMALTENANGO: Chimaltenango Experimental Station, 2,000 m, 5 Nov. 1971, *A. Molina R. & A. R. Molina 26919* (MICH); DEPT. HUEHUETENANGO: ca. 5 mi. WNW of Huehuetenango, 23 Oct. 1976, *T. F. Stuessy & R. C. Gardner 4318* (TEX); DEPT. SACATEPÉQUEZ: slopes of Volcán de Agua, S of Santa María de Jesús, 1,800–2,100 m, 10 Dec. 1938, *P.C. Standley 59378* (MICH).

This new taxon is morphologically intermediate between *Trigonospermum annuum* McVaugh & Laskowski and *T. melampodioides* DC. (Table 1). Most importantly, it differs from *T. annuum* in ray corolla length, disk floret number, anther length, and achene length. It differs from *T. melampodioides* in pubescence of lobes of the disk corollas and outer pales.

The morphologically intermediate nature of *T. stevensii* could be due to interspecific hybridization, but two observations argue against this. First, pollen stainability of the specimens is high (99% of 500 grains in cotton-blue in lactophenol), and the pollen grains appear normal. Second, the possible parents, *T. melampodioides* and *T. annuum*, occur in Mexico reaching only as far south as Oaxaca, and therefore do not occur within the range of *T. stevensii*. This new species, in fact, is allopatric to all other taxa in the genus. These considerations further suggest specific recognition for *T. stevensii*. Additional fieldwork could alter this viewpoint, however, as well as concepts of other poorly collected taxa in the rest of the genus (e.g., *T. auriculatum* Turner).

The discovery of *Trigonospermum stevensii* in Nicaragua extends the range of the genus southward into Central America, previously known only from Mexico and Guatemala. The new species is named in honor of Dr. Warren Douglas Stevens,

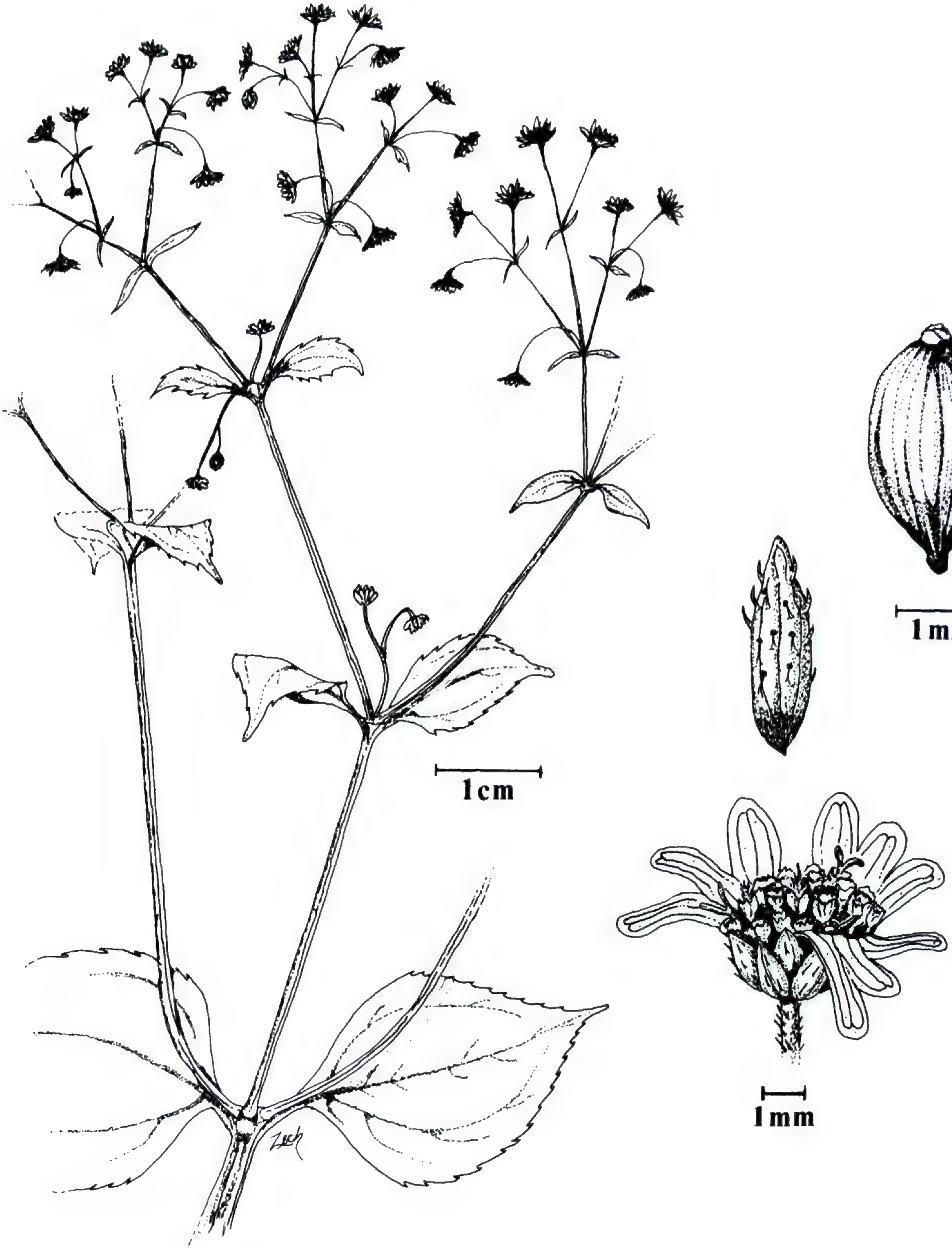

FIGURE 1. *Trigonospermum stevensii*, showing habit, capitulum (with facing ray floret removed), and outer phyllary and achene (same scale). All *Stevens & Grijalva 16156* (holotype).

who is coordinating the *Flora de Nicaragua* project.

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TABLE 1. Comparison of *Trigonospermum stevensii* with *T. annuum* and *T. melampodioides*.

Character	*T. annuum*	*T. stevensii*	*T. melampodioides*
Duration	annual	annual	perennial
Inner phyllary			
Vestiture	glabrous	glabrous	strigose
Margin	apically ciliate	apically fimbriate-ciliate	apically erose
Ray floret			
Number	3–4	3–4	(4–)5(–10)
Style branch length (mm)	0.4–1	0.5–1.4	0.9–1.5
Ligule length (mm)	1.5–3.5	4.5–7	5–8.4
Achene length (mm)	2.8–3.8	2.5–3.2	1.8–3
Disk floret			
Number	8–13	18–25	19–50
Corolla lobe vestiture	sparsely pubescent	sparsely pubescent or glabrous	densely pubescent
Anther length (mm)	0.5–1	1.1–1.3	0.8–1.3

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TWO NEW SPECIES OF *MONOTAGMA* (MARANTACEAE) FROM THE VENEZUELAN GUAYANA

Two new species are described. One is from eastern Bolívar, Venezuela, and is related to *Monotagma spicatum* (Aubl.) Macbr. The other species is related to *Monotagma laxum* (Poepp. & Endl.) K. Schum. but is confined to white sand areas. Inflorescence terminology follows Andersson (1976).

Monotagma ovatum Hagberg, sp. nov. TYPE: Guyana: Pakaraima Mts., Mt. Membaru (5°57′N–60°33–34′W), 600 m, 12 Nov. 1979, *Maas & Westra 4329* (holotype, U; isotypes, BRG not seen, GB, K, NY). Figure 1.

Herba rosulata 0.5–0.7 m alta. Folia basalia 1–4; ultimum folium cum lamina ovata, ad basin obtusa, ad apicem acuminata ad caudata, obliqua, 22–32 × 9–15 cm, adaxiali pagina supra totam superficiem hirtella praeter costam glabra vel solum ad apicem hirtella, abaxiali pagina glabra supra totam superficiem vel ad apicem hirtella; pulvino glabro, 1.2–2.6 cm longo, annulato; petiolo glabro, 6–45 cm longo; vagina papyracea ad chartacea, 14–30 cm longa. Synflorescentia phyllomate bracteato 3.6–5.4 cm longa subtenta, raro frondoso, 3–6 nodis et 6–17 florescentiis, pedunculo 17–55 cm longo. Florescentia principalis 6–11 cm longa, usque 17 spathis, pedunculo 1.1–1.5 cm longo; infima spatha 2.5–3.4 cm longa, flavovirens, papyracea. Sepala 11–14 × 1–3 mm; tubus corollae 20–27 mm longus et 1–2 mm latus, extra glaber vel raro parce pilosus, intra hirsutus, parte basali excepto, lobi virelli, 5–8 × 2–4 mm; staminodium exterius aurantiacum, 6–7 × 2–3 mm; staminodium callosum 4–6 × 3–4 mm, cum parte specifica callosa, sine parte petaloidea; ovarium glabrum, (1–)2–3 mm longum. Capsula 9–12 × ca. 3 mm; semen 8–12 × 2–3 mm (arillo incluso); arillus cum duobus lobis, 2–3 mm longus.

Herb 0.5–0.7 m tall. Rhizomes branched to form clusters of a few shoots, each shoot with 1–4 basal leaves. Ultimate basal leaf with sheath 14–30 cm long, papyraceous to chartaceous, glabrous or slightly appressed-pilose along the margins; petiole 6–45 cm long, flattened laterally, glabrous; a prominent annulus present between petiole and pulvinus; pulvinus 1.2–2.6 cm long, flattened laterally, glabrous; blade 22–32 × 9–15 cm, ovate, chartaceous, broadly obtuse at base, acuminate to caudate at apex, oblique (apex displacement 1.8–3.7 cm), adaxial surface not papillose, hirtellous throughout or at least at apex, midrib glabrous, abaxial surface not papillose, glabrous or rarely appressed-pilose at apex. Inflorescence a 3–6-nodate synflorescence with 6–17 florescences, lowermost node with a bladeless sheath 3.6–5.4 cm long or rarely with a leaf, subsequent nodes with bladeless sheaths, first internode 2.5–11.5 cm long, peduncle 17–55 cm long, glabrous or sparsely hirtellous to hirsute, hairs sometimes appressed. Main florescence 6–11 cm long with 5–17 distichous to unilaterally arranged spathes, first internode 0.8–1.4 cm long, peduncle 1.1–1.5 cm long; lowermost spathe 2.5–3.4 × 0.8–1.2 cm, yellowish green, chartaceous, abaxially glabrous or hirtellous at apex, or rarely hirtellous throughout. Florescence component with 4–5 one-flowered cymules; first prophyll 12–17 mm long, abaxially glabrous or sparsely hirtellous throughout or only at apex or at base, ecarinate; interphylls and bracteoles absent. Pedicel 1–2 mm long; sepals 11–14 × 1–3 mm; corolla tube 20–27 mm long and 1–2 mm wide, yellowish, glabrous to rarely slightly hirsute outside, inside hirsute except for a glabrous basal portion; lobes 5–8 × 2–4 mm, greenish; outer staminode 6–7 × 2–3 mm, orangish with entire apex; fertile stamen 3–5.5 mm long, petaloid appendage absent, theca ca. 1 mm long; inner staminodes reddish, at least toward base; callose staminode 4–6 × 3–4 mm, with a shelf-shaped callus 2–4 mm from apex, without petaloid appendage; cucullate staminode 3–6 mm long, lateral appendage ca. 1 mm long; ovary (1–)2–3 mm long, glabrous; style 2–5 mm long. Capsule 9–12 × ca. 3 mm; seed 8–12 × 2–3 mm, with a 2–3 mm long two-lobed aril.

Distribution and habitat. Known only from the Pakaraima Mountains in Guyana and from adjacent parts of Venezuela. It has been found in crevices and at bases of rocky escarpments and on moss-covered boulders; in Guyana, associated with the fern *Pterozonium* (Maas, pers. comm.), 500–1,300 m.

Monotagma ovatum is closely related to *Monotagma spicatum* (Aubl.) Macbr. but differs by hav-

FIGURE 1. *Monotagma ovatum, Maas & Westra 4432* (U).—A. Inflorescence.—B. Outline of ultimate basal leaf.

ing ovate (vs. elliptic) leaves, less than 10 cm (vs. over 11 cm) from the base to the broadest part of the blade, midrib both adaxially and abaxially glabrous (vs. pilose), pulvinus glabrous (vs. puberulent throughout or at least adaxially), main florescence peduncle 1.1–1.5 cm (vs. 0.4–0.9(1.2) cm), corolla tube 20–27 mm (vs. 17–23 mm) and outer staminode orangish (vs. bluish, fide coll.).

Additional specimens examined. GUYANA: Pakaraima Mts., Mt. Korak, Mazuruni River, 5°59′N–60°37′W, 600 m, Nov. 1979, *Maas & Westra 4432* (BRG not seen, GB, U). VENEZUELA. BOLÍVAR: Cerro Venamo, Jan. 1964, *Steyermark et al. 92723* (US, VEN); El Dorado, Apr. 1957, *Couret 178* (US); El Dorado–Sta. Elena km 105, Dec. 1956, *Foldats 2680* (F, US, VEN, mixed coll., specimen in MY = *M. spicatum*); El Dorado–Sta. Elena km 107, Aug. 1957, *Trujillo 3520* (MY, U); El Dorado–Sta. Elena km 130, Feb. 1968, *Bunting 3017* (MY).

Monotagma vaginatum Hagberg, sp. nov. TYPE: Brazil. Amazonas: about 5 km N of Presidente Figueiredo on the Manaus–Caracaraí road (BR-174), 8 Mar. 1986, *Andersson & Hagberg 1750* (holotype, INPA; isotypes, GB, K, NY, S). Figure 2.

Herba rosulata 0.5–1.7 m alta. Rhizoma ± erecta, in parte supraterranea. Folia basalia 5–25, spirodistichae; ultimum folium cum lamina anguste ovata, ad basin cuneata ad obtusa, ad apicem acuminata ad caudata, centrica ad subcentrica, 20–51 × 2.4–13.5(–16.5) cm, adaxiali pagina hirtella ad puberula secus costam, nervos laterales majores, margines et ad apicem, vel solum secus costam et ad apicem, epidermide papillosa vel non papillosa, abaxiali pagina glabra supra totam superficiem vel ad apicem hirtella, epidermide nonpapillosa; pulvino supra puberulus, 0.7–2.8(–4) cm longo; annulo hirsuto vel deest; petiolo destituto; vagina chartacea ad coriacea, 18–65 cm longa. Synflorescentia phyllomate frondoso subtenta, 2–6 nodis et (3–)5–20(–25) florescentiis, pedunculo (10–) 13.5–50 cm longo. Florescentia principalis 10–25 cm longa, usque 24 spathis, pedunculo 1.2 2.4(–3.3) cm longo; infima spatha 2.6–3.6(–3.9) cm longa, viridis ad flavovirens, chartacea, glabra. Sepala 6–12 × 1–2(–3) mm; tubus corollae 21–30 mm longus et 1–2 mm latus, extra glaber vel raro parce hirsutus, intra hirsutus, parte basali excepto, lobi virelli, 4–8(–10) × 2–5 mm; staminodium exterius album, 6–13 × 4 7 mm; staminodium callosum 4–9 × 3–7 mm, cum parte specifica callosa, sine parte petaloidea; ovarium vertice puberulum, 1–3 mm longum. Capsula (9–)13–20 × 3–4.5 mm; semen (8.5–)12.5–19 × 2–4.5 mm (arillo incluso); arillus cum duobus lobis, 2–4.5 mm longus.

Herb 0.5–1.7 m tall. Rhizomes ± erect, partly aboveground, subtended by "stilt" roots, branched to form clusters of 3–5 shoots, each shoot with 5–25 spirodistichous basal leaves. Ultimate basal leaf with sheath 18–65 cm long (6.5–37.5 cm in cauline leaf), chartaceous to coriaceous, ± glabrous or appressed-hirsute along margin, distally auriculate and furnished with a hair tuft; petiole absent; a hirtellous annulus usually present between sheath and pulvinus; pulvinus 0.7–2.8(–4) cm long, light green, laterally ± flattened, puberulent to hirtellous adaxially, hairs sometimes appressed; blade 20–51 × 2.4–13.5(–16.5) cm [(12.5–)16.5–41(–54.5) × 2.3–12.3(–14) cm in cauline leaf], length from base to broadest part (2.9–)6–13.5(–18) cm, very narrowly to narrowly ovate, chartaceous to coriaceous, markedly scalloped, cuneate to obtuse at base, acuminate to caudate at apex, centric to slightly excentric (apex displacement rarely to 3.5 cm), adaxial surface usually not papillose, dark green, hirtellous to puberulent on midrib, major lateral veins, margins, and apex (or at least on midrib and apex), abaxial surface not papillose,

FIGURE 2. *Monotagma vaginatum.*—A. Habit (from the type population, *Andersson & Hagberg 1750*).—B. Terminal part of a florescence with spathes and a flower (scale = 2 cm, *Hagberg & Medin 361*).

glossy green, glabrous or somewhat hirtellous at apex. Inflorescence a 2–6-nodate synflorescence with (3–)5–20(–25) florescences, lowermost node (sometimes also second and third node) with a cauline leaf, subsequent nodes with bladeless sheaths, first internode 2.7–12.5 cm long, peduncle (10–) 13.5–50 cm long, appressed-pilose or rarely ± glabrous. Main florescence 10–25 cm long with 8–24 distichous spathes, first internode 1–2 cm long, peduncle 1.2–2.4(–3.3) cm long; lowermost spathe 2.6–3.6(–3.9) × 0.7–1.1 cm, greenish to yellowish green, chartaceous, glabrous or rarely puberulent abaxially at apex. Florescence component with 3–5 one-flowered cymules; first prophyll 13–19(–21) mm long, abaxially glabrous, ecarinate; interphylls rarely present; bracteoles absent. Pedicel 1–2 mm long; sepals 6–12 × 1–2(–3) mm, translucently white; corolla tube 21–30 mm long and 1–2 mm wide, white, outside glabrous or rarely hirsute above tip of sepals, inside hirsute except for a glabrous basal portion, lobes 4–8(–10) × 2–5 mm, white to pale green; outer staminode 6–13 × 4–7 mm, white, spathulate with entire apex; fertile stamen 3–8 mm long, petaloid appendage absent, theca 1–2 mm long; callose staminode 4–9 × 3–7 mm, white, sometimes green toward apex, with a shelf-shaped callus 2–4 mm from apex, without petaloid appendage; cucullate staminode 3–6 mm long, white, lateral appendage 1–2 mm long; ovary 1–3 mm long, puberulent apically; style 3–6 mm long, back of style turning red when tripped. Capsule (9–)13–20 × 2–4.5 mm; seed brownish, (8.5–)12.5–19 × 2–4.5 mm, with a whitish, 2–4.5 mm long two-lobed aril.

Distribution and habitat. Monotagma vaginatum occurs in the white sand forests (Amazonian caatingas/campinas) around Iquitos, Peru; in southern Venezuela and adjacent parts of northwestern Brazil; around Manaus, Brazil; in scattered

campina areas in eastern Acre, Brazil; and in Pará, Brazil. It has also been found in the coastal forest in the basin of the Oyapock River and on Piton Rocheux in French Guiana.

Monotagma vaginatum is related to *Monotagma laxum* (Poepp. & Endl.) K. Schum. from which it differs by having rhizomes partly aboveground (vs. on ground level), basal leaves spirodistichous (vs. distichous or shoot apex irregularly twisted), mature shoots with 5–25 (vs. 1–7(–15)) basal leaves, which are comparatively narrower [length/width (3–)3.7–8.5 vs. 2.75–4.5(–5.5) cm], petiole absent (vs. present) and sepals 6–12 (vs. 9–17 mm) long.

Additional specimens examined. BRAZIL. ACRE: 11 km S of Rio Branco, Oct. 1980, *Lowrie et al. 628* (GB, INPA); 12 km S of Rio Branco on road to Xapuri, Oct. 1980, *Cid & Souza 3030* (INPA); 5 km E of Sena Madureira, Oct. 1968, *Prance et al. 7789* (F, GH, INPA, K, MG, NY, S, U). AMAZONAS: 12 km up on Rio Cuieiras, Feb. 1969, *Kennedy 112* (DUKE, GB); 50 km up on Rio Cuieiras, Apr. 1974, *Ongley & Ramos P21782* (INPA, NY); 3 km S of Serra Central da Serra Aracá, Feb. 1984, *Amaral 1674* (GB); 62 km S of Presidente Figueiredo on road BR 174, Mar. 1986, *Andersson & Hagberg 1754* (GB, INPA, S); between Rio Tupana and Castanha, on road Manaus–Porto Velho, July 1972, *M. F. Silva et al. 883* (INPA); INPA reserve, 45 km N of Manaus on BR 174, Dec. 1977, *A. B. Anderson 321, 339* (INPA); Manaus, 1877, *Jobert 430* (P); Aug. 1957, *Rodrigues 480* (INPA); Jan. 1963, *E. Santos 1487* (GB); Feb. 1960, *de la Sota 2459* (LIL); Feb. 1901, *Ule 5415* (G, HBG, MG); Manaus, 5 km N of airport on road to Itacoatiara, Mar. 1986, *Andersson & Hagberg 1773* (GB, INPA); Manaus, Igarapé do Pensador, Oct. 1955, *Rodrigues 2133* (INPA); Manaus, Ponta Negra, 1971, *Prance et al. 11683* (GB, GH, INPA, MG, NY, U); Manaus, near Parque 10, Sep. 1971, *Maas & Maas 277* (INPA, K, MO, U); near Manaus, Dec. 1964, *Vogel 288* (U); Manaus–Caracaraí (BR 174) km 130, Dec. 1974, *Gentry 12966* (INPA, MO); Nov. 1973, *Berg et al. P19525* (GB, INPA); Feb. 1974, *Steward et al. 20294* (GB, INPA); Manaus–Caracaraí km 131, Mar. 1974, *Loureiro et al. s.n.* (INPA); Manaus–Caracaraí km 60, INPA reserve, July 1976, *Kirkpatrick 106* (INPA); Oct. 1976, *Kirkpatrick 118* (INPA); Manaus–Caracaraí km 10, Oct. 1966, *Prance et al. 2711* (F, K, INPA, MG, NY, S, U, UBC, UC); Marabitanas, Rio Negro, Apr. 1947, *Pires 476* (IAN); Porto Camanaus, Oct. 1978, *Madison et al. 389* (INPA); Rio Xeriuini, Apr. 1974, *Pires 13997* (INPA, MG); São Gabriel da Cachoeira, Mar. 1975, *M. R. Cordeiro 435* (IAN); São Gabriel, airport, Oct. 1978, *Madison et al. 506* (INPA, MG, US); Tunuí, Içana, Oct. 1947, *Pires 711* (IAN, NY); above Santa Isabel do Rio Negro, Oct. 1971, *Prance et al. 15381* (GB, INPA, NY, U); junction of Rio Cuieras and Branquinho, Apr. 1974, *Campbell et al. P21926* (INPA, NY); mouth of Rio Caiari, Sep. 1952, *Fróes & Addison 28648* (IAN). PARÁ: 17 km S of Ligação do Pará on road Belém-Brasilia, Mar. 1980, *Plowman 9398* (MG); 40 km SW of Marabá, on road PA 150, Dec. 1981, *Daly et al. 1693* (GB); Paragominas, Tingi do Pará, Dec. 1979, *Maciel et al. 466* (MG); Tucuruí, Oct. 1977, *A. S. Silva et al. 173* (K, MG, MO, NY, S); km 324 on road Belém–Brasilia, Aug. 1960, *Oliveira 1013* (IAN); km 174 on road Belém–Brasilia, May 1960, *Oliveira 664* (IAN). COLOMBIA. GUAINIA: San Felipe, Nov. 1952, *Humbert 27441* (P). FRENCH GUIANA: Crique Gabaret, basin of Oyapock River, Apr. 1988, *Cremers 9929* (GB); Piton Rocheux, Crique Armontabo, Feb. 1981, *Cremers 7044* (GB, P). PERU. LORETO: Brillo Nuevo, Río Yaguasyacu, Apr. 1977, *Plowman et al. 6806* (F, GH); Lago Llanchama, near Río Nanay, Aug. 1972, *Croat 18714* (MO); Mishana on Río Nanay, Jan. 1976, *Gentry et al. 15837* (F, MO); Feb. 1987, *Hagberg & Medin 361* (AMAZ, F, GB), *365* (AMAZ, F, GB, U); July 1984, *Vásquez et al. 5298* (GB); Nauta, June 1984, *Vásquez & Jaramillo 5090* (GB); Pto. Almendras, SW of Iquitos, May 1974, *Andersson 15* (GB); Quistococha, near Iquitos, Nov. 1940, *Asplund 14662* (S), *14663* (S); Dec. 1979, *Davidson & Jones 9685* (GB); May 1978, *Gentry & Jaramillo 22304* (GB). VENEZUELA, AMAZONAS: Cerro Aracamuni, Quebrada Camp, Oct. 1987, *Liesner & Carnevali 22327* (GB); Oct. 1987, *Liesner & Delascio 22249* (GB); Cerro de La Neblina, ESE slope above Río Mawarinuma, Apr. 1984, *Thomas 3248* (GB); IVIC study site, 4 km NE of San Carlos de Río Negro, Apr. 1979, *Liesner 6157* (GB, MO, VEN); Mamurividi, Río Pacimoni, June 1984, *Davidse & Miller 26714* (GB); Mucuriapi, lower Río Baria, June 1984, *Davidse & Miller 26746* (GB); Río Mawarinuma, 3–5 km NE of Cerro de La Neblina base camp, Mar. 1984, *Liesner 16344* (GB); Río Pacimoni, Apr. 1970, *Steyermark & Bunting 102457* (MY, NY, VEN); San Carlos de Río Negro, July 1989, *Bunting et al. 4137* (MY, U); Jan. 1968, *Wessels Boer 2343* (GB, U); San Carlos de Río Negro, near airport, Apr. 1970, *Steyermark & Bunting 102767* (GB, US, VEN); 0–0.5 km NE of San Carlos de Río Negro, Nov. 1977, *Liesner 3683* (VEN), *Liesner 3684* (MO); 5 km S of San Carlos de Río Negro, Apr. 1979, *Liesner 6495* (MO, VEN); Solano, Brazo Casiquiare, June 1984, *Davidse & Miller 26662* (GB).

I thank Lennart Andersson, who proposed *Monotagma* as a subject for my doctoral thesis and who critically read the manuscript. The field studies were supported by grants from the Royal Swedish Academy of Sciences (A. F. Regnells Botaniska Gåvomedal, K. O. E. Stenströms Fond, and P. F. Wahlbergs Minnesfond), W. & M. Lundgrens Vetenskapsfond, Kungl. och Hvitfeldska Stipendieinrättningen (Överskottsfonden) and Anna Ahrenbergs Fond.

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—Mats Hagberg, *Department of Systematic Botany, Gothenburg University, Carl Skottsbergs Gata 22, 41319 Göteborg, Sweden.*

BOOK REVIEW

Oostendorp, Cora. The Bryophytes of the Palaeozoic and the Mesozoic. 1987. Bryophytorum Bibliotheca, Band 34. 112 pp., 49 pls. J. Cramer, Stuttgart. ISBN 3-443-62006-X. Retail price: 120 DM.

This comprehensive catalog of Paleozoic and Mesozoic fossil bryophytes collates all published literature up to 1980. Many of the original illustrations are reproduced photographically in the plates at the end of the book. Only gametophytic material or sporophytes attached to gametophores, described or annotated recently as bryophytic, have been included. A few incertae sedis, questionable bryophyte-like fossils, are also included. Russian and Polish but not the original Latin or French diagnoses have been translated into English. For each form species (not assigned to an extant family) in the alphabetized list, Oostendorp lists the nomenclatural authority and a reference to the illustrations reproduced in the back of the book. This is followed by a list of synonyms with publication references according to the *International List of Periodical World Abbreviations* (1968). Each form species is then treated further under four subheadings: (1) **Icones**, a list of publications with original or reproduced figures; (2) **Type**, including the location of the collection in which the holotype is deposited and the field locality, stratigraphical position, and age of the type collection; (3) **Diagnosis**, sometimes presented as **Original Diagnosis** and an additional **Description**, or **Diagnosis** and **Diagnosis emended**, with reference to the original publication; and (4) **Systematic Position**, to order if known. Form genera are treated similarly to form species with the subheadings **Type-species**, **Diagnosis**, and **Systematic position**.

After a brief section on problematic bryophyte-like fossils, treated similarly to the form species, there follows an exhaustive reference list and index, the latter differentiating among accepted names (130), synonyms, and new combinations (four new combinations made by C. Oostendorp).

Preceding the lists described above are brief introductory chapters on "History and Classification" and on "The Fossil Record." The first chapter discusses the development of Paleozoic and Mesozoic paleobryology and defines the structural characteristics of the form genera. It also classifies form genera with well-preserved remains within the present classification of bryophytic orders, following the *International Code of Botanical Nomenclature*. Only one order, the Protosphagnales, does not have any extant members. Table 3 lists chronologically all described species with their synonymy of the form genera *Thallitis*, *Hepaticites*, *Jungermannitis*, *Metzgeriites*, *Marchantites*, and *Muscites*.

The chapter summarizing the fossil record reviews chronologically the major form species for each geological period from the Devonian to Cretaceous. In addition, it lists all well-preserved form genera and species of each period for each order in a systematic review. This is the only part of the book where an attempt is made to evaluate some records in the light of bryophyte phylogeny and classification. Conclusions derived from this analysis are brief and general, without any deviation from commonly accepted concepts suggested in earlier review papers.

In my own database I have been unable to find additional records published before 1980 that were not collated in this book. The number of typographical errors is very small. The larger tables are not well differentiated from the main text, and headings are frequently separated by page breaks from the following text. The gray-toned photographic reproductions of the figures are a major improvement over the photocopies of the less accessible publications I have often had to study. The selection of figures reproduced for the plates is sufficient and representative. With such a large amount of disparate material to catalog and analyze, C. Oostendorp was not able to evaluate critically every record. However, this book will be invaluable as a starting point for the study of the relationship between fossil bryophytes and phylogenetic research on living mosses and liverworts.—Jan A. Janssens, *Department of Ecology, Evolution, and Behavior, 318 Church Street, University of Minnesota, Minneapolis, Minnesota 55455, U.S.A.*

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THE PUBLICATION OF THE *FLORA OF CHINA* WILL BE A GREAT CONTRIBUTION TO THE SCIENTIFIC CIRCLES OF THE WORLD

Opening speech by
Professor Wu, Zheng-Yi[1] at the
second editorial meeting for the
joint *Flora of China* project,
Guangzhou, Guangdong, China,
August 1989

The first book of the *Flora Reipublicae Popularis Sinicae* (FRPS) (volume 2) was published as a gift to the tenth anniversary of the People's Republic of China (Ching, 1959). Thirty years have passed since then. Although we lost seven years during the Cultural Revolution, Chinese botanists have worked hard under various difficult conditions. Up to now, more than half of the FRPS has been published or is in press. Most of the remaining volumes have been completed, and only a few are in the middle stages of writing. The complete work is planned to be published within ten years; thus we shall give this monumental work to the world in the year 2000. While the FRPS is being prepared, botanists in every province or district are very actively preparing floras of their own regions. For example, the floras of Hainan, Jiangsu, Hubei, Xizang, and the herbaceous plants of northeast China have been published. *Flora of Mount Henduan* has been submitted to the publisher. Floras of the remaining provinces or districts are presently being written or are partially published. These floras have added or will add new information to the FRPS. For various reasons very few plant specimens from Taiwan and Hongkong have been available as we compile the FRPS. We have had to use information in the literature in cases when herbarium materials are inadequate. Problems that still could not be solved have had to be set aside until additional information is available. We are very glad that the *Flora of Taiwan* has been completed and now is being revised, and that the *Flora of Hongkong* is being compiled under the direction of Dr. Shiu-ying Hu at the Chinese University of Hongkong. We would like to thank members of the biology department of the Chinese University of Hongkong and Dr. Shiu-ying Hu for giving many excellent plant specimens to the herbarium of the Institute of Botany at Beijing. We hope that in the near future our colleagues in Taiwan can give us Taiwanese plant specimens or can exchange specimens with us.

The *Flora of China* (FOC) is a joint project by Chinese and American botanists and is based on the FRPS. The FOC will be another monumental work, in English and different from the FRPS. FOC

[1] Director Emeritus, Kunming Institute of Botany, Academia Sinica, Kunming, Yunnan, People's Republic of China.

will have more or less complete information on specimens from Hongkong and Taiwan. The Chinese and American botanists have experience writing floras of large areas, so we are confident that the joint project can be carried out as planned and that the *Flora of China* can be published. It will be useful to persons worldwide who are concerned with Chinese plants. We thank the Chinese government's open policy, which has made this joint project possible, has given us the opportunity to make friends with our foreign colleagues, and has allowed scientific exchange with our Hongkong and Taiwan colleagues. Our academic exchange and cooperation with colleagues in America and other countries has promoted and will continue to promote the progress of science in China. When we are together with our American and Hongkong colleagues today, we are very pleased that the FRPS is near completion, floras of various provinces and districts in China are coming up like bamboo shoots after a spring rain, the *Flora of Taiwan* is under revision for a second edition, and the *Flora of Hongkong* is being written.

The achievement in plant systematics in China has also promoted the development of plant floristic geography. China has a rich flora that not only has an ancient origin, but also has a very complicated history of migration and merging. The Chinese flora has attracted the attention of botanists all over the world. Many foreign scholars have come to China to investigate and study the flora of China during the last century. Since the 1920s, the Chinese botanists Hsen-Hsu Hu, Tcheng-ngo Liou, and Hui-lin Li have published many books and articles on the Chinese flora, probing into the origin of the flora of certain regions in China and the relationships between the flora of East Asia and North America (Hu, 1936, 1948; Li, 1944, 1950, 1952, 1953a–c, 1957; Liou, 1934, 1944, 1955). These botanists made great contributions, but because the floras of many regions were not known in great detail, the conclusions they made were unavoidably simple and sketchy. With the large-scaled field expeditions after 1949, we have collected a large number of plant specimens, which have made possible the publication of many monographs on plant genera and families. Compiling the FRPS and floras of various provinces and districts has laid the foundations for studying the flora of China.

I have preliminarily summarized previous work on the flora of China and described the floristic characteristics of the distributional types and subtypes of Chinese seed plants, and their integrating relationships (Wu, 1963, 1965; Wu & Wang, 1983). Professor Zhang, Hong-da of Sun-yat-sen University also has published an article on the origin and development of the Chinese flora in which he differs from my opinions (Zhang, 1980). In order to make a thorough study of the Chinese flora, I proposed a research project—Study on the Chinese Flora—and applied to the Natural Science Foundation of China (NSFC). The committee of the NSFC has attached importance to this project and is about to approve it.[2] Most participants in this project are the main authors of the FRPS. I believe that our colleagues from Hongkong and Taiwan will also be interested in this project. Although they cannot participate in it for the time being, they can observe and comment, and they have academic exchanges with us. We hope that in the near future we can build another milestone in our rich and beautiful motherland and make even greater contributions to scientific knowledge.

Our American friends have given us a lot of help in promoting the development of botany in China. We have exchanged visiting scholars, exchanged plant specimens, and cooperated with each other very well. The joint Sino-American project of *Flora of China* is a typical example. In October of last year under the *Metasequoia* trees at the Missouri Botanical Garden, Dr. Peter Raven and I cosigned an agreement for this joint project. The preparation has proceeded smoothly for almost one year. For example, the project has been approved by the National Science Foundation (NSF) of the United States, and the publication problem has been resolved. Cooperation between the American and Chinese members of the joint Editorial Committee, especially between Dr. William Tai (the project coordinator) and Professors Dai, Lun-kai (acting member of the joint Editorial Committee) and Cui, Hong-bin (deputy editor-in-chief of the FRPS and a member of the joint Editorial Committee), has been very successful. They have made great efforts to reach a mutual understanding by overcoming various difficulties caused by the different customs and systems in our two countries. They have arranged for volume 17 to be a test treatment followed by volumes 15 and 16. They also selected the Chinese and American authors for the remaining volumes and helped these authors contact one another. The authors of the seventeenth volume: Professors Chen, Shou-liang (Verbenaceae), Li, Xi-wen (Laminaceae), and Lu, An-min (Solanaceae) are due gratitude. The first two

[2] Subsequent to this meeting, NSFC approved the project.

authors have finished their manuscripts. The first product of our joint project is to come out at the end of next year or in the beginning of the year after next. Professors Chen, Shou-liang and Li, Xi-wen have had questions when preparing the treatments. This is the exact purpose of the test treatment. We can discuss these problems at this meeting and modify the author's guidelines accordingly.

We realize that it will be a very complicated process to accomplish this monumental work. It will involve many people and many related projects. Every plant family has its own characteristics, and every author will have questions. According to our experiences, the authors' guidelines need to be modified as the writing continues. We need overall regulations on how to cooperate with each other and how to translate and edit the *Flora*, and both sides should abide by them. At the same time, we should be flexible and try to solve specific problems with specific methods under the direction of the joint Editorial Committee. We should also have regulations on how to regulate loaning and collecting specimens and gathering references. These questions should be discussed at this meeting. The Editorial Committee of the FRPS has an office in Beijing. This office is also responsible for the work of the Chinese side of the joint Editorial Committee.

It is a pleasure to meet Professor Paul Butt of the Chinese University of Hongkong at this meeting. It is unfortunate that our colleagues from Taiwan have not been able to meet with us in Guangzhou. But we welcome our colleagues to come to the mainland for visiting or research at any time. We also hope that we can visit Taiwan someday. I have been conducting floristic studies for many years and have visited every region in China except Taiwan. It will be a pity if I cannot visit there in my lifetime.

We would like to thank the host—the South China Institute of Botany at Ghangzhou, particularly Professor Lin, Yeou-ruen, who arranged everything necessary for the meeting in a very short time. Although the meeting could not be held in Hongkong as planned, we give our sincere appreciation to Professor Paul Butt and Professor Chang Shu-ting, his department head, for their excellent preparations for the meeting.

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SYSTEMATICS OF *LAPEIROUSIA* (IRIDACEAE–IXIOIDEAE) IN TROPICAL AFRICA[1]

Peter Goldblatt[2]

ABSTRACT

The genus *Lapeirousia*, a member of the predominantly African subfamily Ixioideae of Iridaceae, is one of five genera of tribe Watsonieae and is the only one that is widespread in southern and tropical Africa. In this revision of the tropical members of the genus, 16 species are recognized, 14 assigned to the largely tropical sect. *Paniculata* (subg. *Paniculata*) and two to the largely temperate southern African sect. *Sophronia* (subg. *Lapeirousia*). One new species, *L. angolensis*, is described and *L. teretifolia* is raised from subspecies to species rank. The center for tropical African *Lapeirousia* is northern Namibia, but species occur across south tropical Africa to Mozambique and north to Ethiopia, Sudan, and Nigeria. *Lapeirousia* is one of few genera well represented in both tropical Africa and the winter-rainfall region of temperate southern Africa, and it is unique in its wide distribution in drier parts of Africa rather than the well-watered eastern highland areas of the continent. Variation among the species is largely floral, and flowers range from completely actinomorphic to medianly zygomorphic and from short-tubed to extremely long-tubed. An unusual degree of chromosomal variation occurs in sect. *Paniculata* with numbers ranging from $n = 8$, 7, 6, 5, 4, to 3 and karyotypes from strongly bimodal to relatively uniform. Chromosome cytology correlates to some degree with patterns of morphological variation and provides independent support for the phylogeny of the tropical species.

Lapeirousia, a member of the largely African subfamily Ixioideae of the Iridaceae, is one of the few genera in the family well represented in tropical Africa and in the southern African winter-rainfall zone of the western Cape Province of South Africa and southwestern Namibia. *Lapeirousia* comprises two subgenera (Goldblatt & Manning, 1990), subg. *Lapeirousia* (17 species—Goldblatt, 1972), largely temperate, and subg. *Paniculata* with sect. *Fastigiata* (5 species—Goldblatt & Manning, in prep.) restricted to the SW Cape of South Africa, and sect. *Paniculata* (15 species) mostly tropical African (Table 1) but extending well into the Transvaal, and with a disjunct species in the SW Cape (Goldblatt & Manning, in prep.). Although centered along the west coast of South Africa, subg. *Lapeirousia* includes two species, *L. odoratissima* and *L. littoralis*, having wide ranges in tropical Africa (Table 1). Of the approximately 38 species in the genus some 21 are restricted to the southern African winter-rainfall area (Goldblatt, 1972), and 16 are largely tropical. Only *L. littoralis* (= *L. caudata*) is widely shared between the two areas. The tropical African species are concentrated in south central Africa, particularly in Namibia, Angola, and Zambia with a decreasing representation in East Africa and Mozambique. Two species reach Ethiopia and one extends to Nigeria.

The taxonomy of *Lapeirousia* in tropical Africa has long been considered problematic, and there has been no complete treatment of the genus outside southern Africa since Baker's study in *Flora of Tropical Africa* (1898). Although completed at a time when tropical Africa was incompletely explored botanically, this revision admitted 14 species of true *Lapeirousia* and four more that are now treated as the genus *Anomatheca*. Since 1898, 21 tropical species have been described, making a total of some 35 for the area. The local floristic treatments published over the past 20 years for *Flora of West Tropical Africa* (Hepper, 1968), Namibia (Sölch, 1969) and Zaire (Geerinck et al., 1972), and a new species described by Wanntorp (1971) represent the only significant contributions

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TABLE 1. The species of *Lapeirousia* in tropical Africa alphabetically arranged within their sections, including a summary of their distributions.

SUBGENUS *PANICULATA* SECTION *PANICULATA*	
L. abyssinica	northern Ethiopia, eastern Sudan
L. angolensis	eastern Angola
L. avasmontana	western and northern Namibia
L. bainesii	central and northern Namibia, southern Angola, Botswana and northwestern Transvaal
L. coerulea	central and northern Namibia, northwestern Botswana
L. erythrantha	eastern Angola, Zambia, southern Zaire, Zimbabwe, Malawi, western and southern Tanzania, Mozambique, northeastern Botswana
L. gracilis	Namibia
L. masukuensis	central Mozambique, eastern Transvaal, southeastern Zimbabwe
L. otaviensis	central Namibia
L. rivularis	Namibia, southern Angola and Zambia
L. sandersonii	central and western Transvaal, eastern Botswana
L. schimperi	northern Namibia, southern Angola, Zambia, Zimbabwe, Tanzania, northern Kenya, Ethiopia, Sudan
L. setifolia	northern Malawi, southwestern Tanzania, Zimbabwe
L. teretifolia	western Zambia, northeastern Angola, southern Zaire
SUBGENUS *LAPEIROUSIA*	
L. littoralis	
subsp. *littoralis*	southwestern Angola, western and southern Namibia, Botswana, northern Cape, western Transvaal
subsp. *caudata*	northern Namibia, Zambia, Zimbabwe, southern Mozambique
L. odoratissima	northern Namibia, southern Angola, Zambia, southern Zaire, Zimbabwe, Malawi, Tanzania

to our knowledge of *Lapeirousia* outside southern Africa. The species of the winter-rainfall zone of southern Africa were revised in 1972 (Goldblatt, 1972) when *Anomatheca*, treated by Baker (1892, 1896, 1898) as a subgenus, was removed from *Lapeirousia* and restored to generic rank.

The present treatment, summarized in Table 2, represents a complete revision of *Lapeirousia* in tropical Africa. This treatment differs substantially in the delimitation of *L. erythrantha* (Geerinck et al., 1972) and includes several changes in the circumscription of species in Namibia (cf. Sölch, 1969). In Namibia I recognize *L. avasmontana* (previously included in *L. coerulea*) and *L. otaviensis* (included by Sölch in *L. bainesii*), whereas I consider *L. bainesii* and *L. vaupeliana* conspecific, although both were recognized by Sölch. The widespread *L. caudata* has an earlier synonym, *L. littoralis*, but I still consider the species to comprise two subspecies, one largely tropical and the other largely temperate (cf. Goldblatt, 1972).

Treatment of the *Lapeirousia erythrantha* complex is difficult and I doubt that any solution will ever be entirely satisfactory. I regard *L. erythrantha* as one widespread and variable species including *L. rhodesiana* and *L. briartii*, but I recognize as distinct *L. sandersonii*, *L. masukuensis*, *L. teretifolia*, *L. setifolia*, and *L. angolensis* (the last-mentioned a new species). Geerinck et al. (1972) treated some of the foregoing species as varieties of *L. erythrantha*.

GENERIC DEFINITION AND RELATIONSHIPS

Lapeirousia is a member of the Old World and largely African subfamily Ixioideae, one of the four subfamilies of Iridaceae (Goldblatt, 1990a). It is currently assigned to tribe Watsonieae (5 genera, ca. 95 species), one of three tribes of Ixioideae (Goldblatt, 1989, 1990a), the others being the monotypic Pillansieae and the large Ixieae, with some 25 genera and over 700 species, nearly half the total for the family. Distinguishing characteristics of Watsonieae are deeply forked style branches, a derived condition (Goldblatt, 1989), and corms produced entirely from a bud near the base of the flowering stem and attached laterally to the flowering axis (Goldblatt, 1990a). The latter is thought to be ancestral to corm development in Ixieae in which the corm is formed, in part, from the base of the flowering stem, and the flowering stem is attached to the corm near the corm apex (Goldblatt, 1989).

Lapeirousia is readily defined by its characteristic corm and corm tunics. The corms of all species are more or less bell-shaped with a flat base or side

(Fig. 1C–H). The tunics are typically hard and cartilaginous to woody and consist of concentric layers of either densely compacted fibers or woody material of uniform texture. Corms of this shape are not found in other Watsonieae but occur in a few genera of Ixioideae where they are found in only a few specialized species of *Romulea* and *Hesperantha* (which coincidentally also have woody corm tunics). The genus probably most closely related to *Lapeirousia* is the monotypic south tropical African *Savannosiphon* Goldbl. & Marais. The two genera share two unusual features in Watsonieae, angular to winged stems and membranous walled capsules. Outgroup comparison suggests that both characters are specialized. *Lapeirousia* and *Savannosiphon* are probably most closely allied to *Thereianthus* and *Micranthus*, two small southwestern Cape genera (Goldblatt, 1989). These four genera form a clade, united by having the foliage leaves inserted on the flowering stem rather than on the corm (Fig. 1B, C); thus the leaves do not contribute to the formation of the corm tunics, as they do in *Watsonia* (the remaining genus of Watsonieae) and in the primitive monotypic Pillansieae.

The evolutionary relationships of *Lapeirousia* are discussed further in the section below dealing with phylogeny.

Geography

Lapeirousia is one of few widespread African genera of Iridaceae that have centers in the winter-rainfall zone of the southern African west coast and in tropical Africa (Fig. 2). This pattern is unusual for Iridaceae, in which most African genera are either restricted to the Cape region of South Africa or occur only in the summer-rainfall parts of eastern southern Africa, sometimes as far north as Ethiopia. Only *Gladiolus*, *Hesperantha*, and *Romulea* (Ixioideae), *Moraea* (Iridoideae), and *Aristea* (Nivenioideae) have ranges comparable to that of *Lapeirousia*. However, all of these genera favor mesic habitats in tropical Africa and occur either in montane and high-plateau areas or in zones of particularly high rainfall. *Lapeirousia* alone has radiated into dry parts of Africa and is well represented in Namibia, adjacent southern Angola, Botswana, and Zambia. Elsewhere in tropical Africa the number of species of *Lapeirousia* decreases rapidly; five species occur in Zimbabwe, three in Mozambique and Tanzania, two in Ethiopia, and one in Sudan and Nigeria.

The area of greatest species concentration is the northern half of Namibia (Fig. 2A). Here the endemic *Lapeirousia avasmontana* occurs locally in the Windhoek area, and *L. gracilis* extends along the length of the country from the Fish River Canyon in the south to the Kaokoveld in the north. *Lapeirousia otaviensis* is nearly endemic, extending from the Erongo Mountains in the central west to southern Angola, and *L. coerulea*, widespread and relatively common in central and northern Namibia, also occurs in the northwest of Botswana. *Lapeirousia bainesii* is particularly common in northern Namibia, but it extends into southern Angola and across Botswana to the northwestern Transvaal. In addition, *L. schimperi*, *L. rivularis*, *L. littoralis*, and *L. odoratissima* occur widely in Namibia as well as elsewhere in tropical Africa. In temperate southern Namibia three more species of *Lapeirousia*, *L. barklyi*, *L. dolomitica*, and *L. plicata*, are predominantly southern African and have a winter-growing and spring-flowering phenology.

A second, minor center for *Lapeirousia* in tropical Africa (Fig. 2B) is western Zambia, southern Zaire, and eastern Angola where two species are endemic, *L. teretifolia* in the north and *L. angolensis* in the south. Also widely occurring in this area are *L. erythrantha*, *L. rivularis*, and *L. littoralis*. Other relatively localized species are *L. abyssinica*, restricted to northern Ethiopia; *L. masukuensis*, central and southern Mozambique, the eastern Transvaal, and southeastern Zimbabwe; and *L. sandersonii*, the central and western Transvaal and eastern Botswana. The tropical African species of *Lapeirousia* are, in general, relatively widely distributed, the most prominent example being *L. schimperi*. This species extends across south tropical Africa from northern Namibia to Zimbabwe and has a series of disjunct populations in northern Tanzania, northeastern Kenya and southern Ethiopia, northern Ethiopia, and western Sudan. *Lapeirousia erythrantha* has a comparable distribution, being common across south central Africa from eastern Angola to the Mozambique coast, and it has a series of populations in northern Nigeria. Unlike *L. schimperi*, *L. erythrantha* consists of a number of distinctive regional populations across its range.

The only species of subg. *Lapeirousia* that occur in tropical Africa, *L. littoralis* and *L. odoratissima*, also have wide distributions, the latter extending from western Angola and Namibia to central Tanzania. This contrasts with the southern African members of the subgenus that have narrow ranges, and in some cases are known from only one or two localities (e.g., *L. montana*, *L. oreogena*, *L. verecunda* [Goldblatt, 1972]).

Such disjunctions as encountered in *L. schim-*

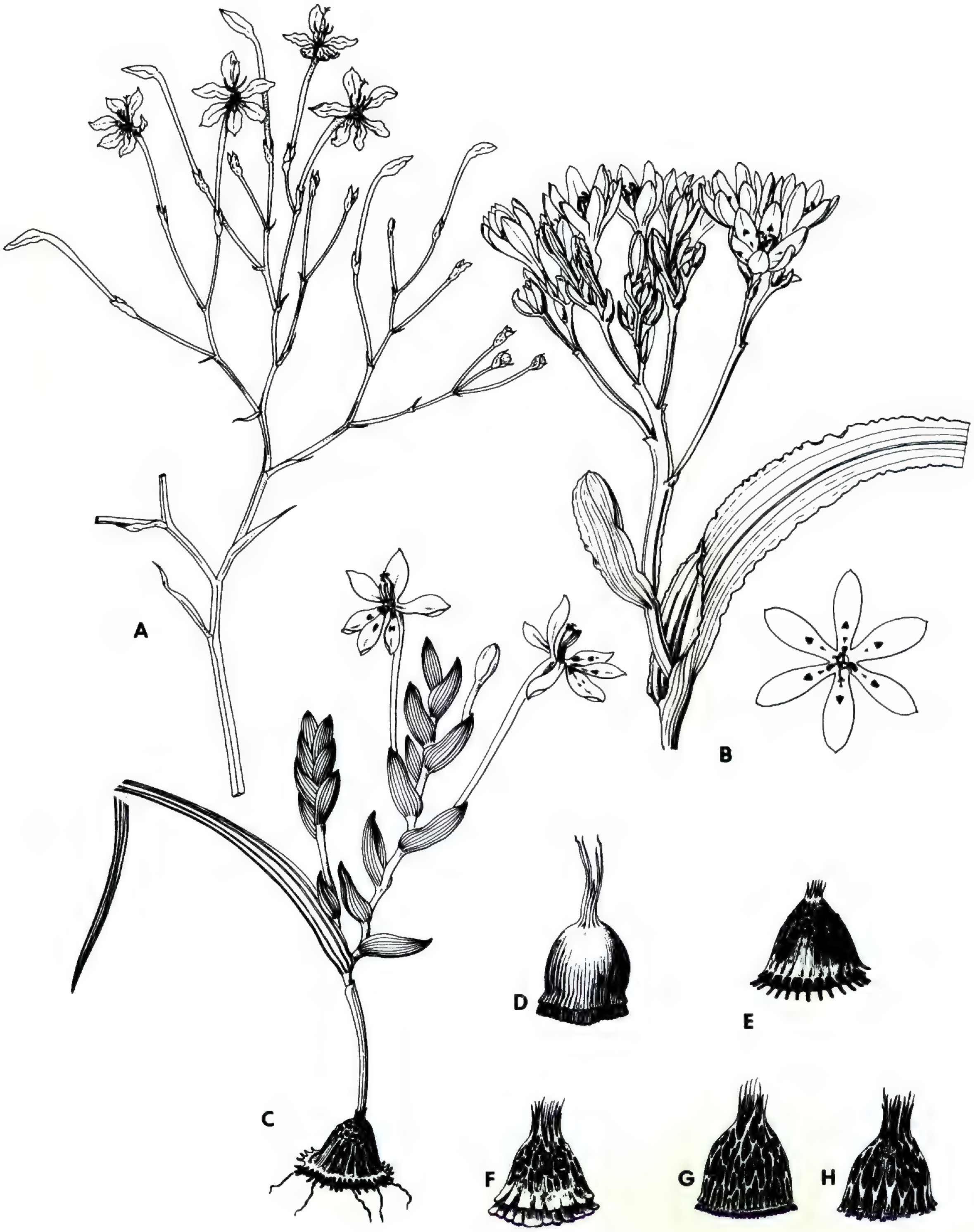

FIGURE 1. Growth forms and main flower and corm types in *Lapeirousia*.—A. *L. bainesii*, divaricately branched pseudopanicle with zygomorphic flowers (subg. *Paniculata* sect. *Paniculata*).—B. *L. corymbosa*, congested pseudopanicle with actinomorphic flowers and plane leaves with midrib (subg. *Paniculata* sect. *Fastigiata*).—C. *L. dolomitica*, branched spike, zygomorphic flowers, and corrugate leaf (subg. *Lapeirousia* sect. *Lapeirousia*).—D. *L. plicata* (subg. *Lapeirousia* sect. *Sophronia*).—E. *L. divaricata* (subg. *Lapeirousia* sect. *Lapeirousia*).—F. *L. micrantha* (subg. *Paniculata* sect. *Fastigiata*).—G. *L. bainesii*.—H. *L. coerulea* (subg. *Paniculata* sect. *Paniculata*). A–C × 0.5, E–H full size. (Drawn by M. L. Branch & J. C. Manning.)

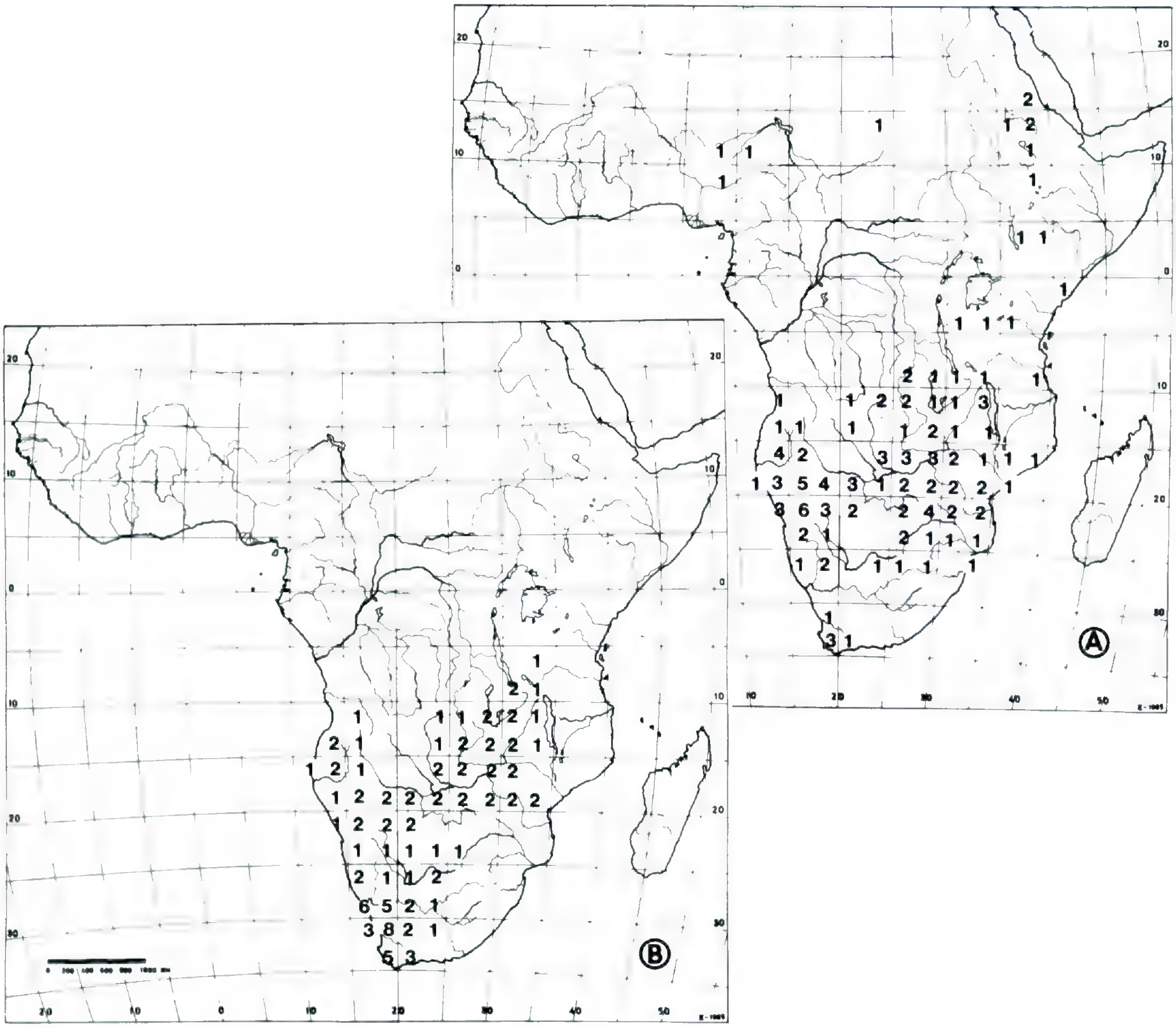

FIGURE 2. Geography of *Lapeirousia*.—A. Distribution of subg. *Paniculata*.—B. Distribution of subg. *Lapeirousia*. Figures represent the number of species recorded in each 2°30′-degree square grid.

peri and *L. erythrantha* are uncommon in Iridaceae, although they are known in a few species in several of the widespread African genera of the family (e.g., *Moraea schimperi*, *Gladiolus dalenii*, and *Hesperantha petitiana* [Goldblatt, 1977, 1986]). However, the pattern of narrow distributions for many species in southern Africa vs. wide ranges for most tropical species is common in Africa and is consistent with patterns for many genera in different families.

MORPHOLOGY

ROOTSTOCK

The most distinctive feature of *Lapeirousia*, and the one that defines it, is the flat-based corm (or more correctly flat-sided corm since the flat portion is oriented obliquely in the ground—Fig. 1). The corms are bell-shaped in all species when not distorted by growing conditions. The corm coverings or tunics reflect the corm shape and consist of a separate basal disc and bell-shaped upper part. Other Ixioideae usually have rounded corms, although a few species of *Romulea* (de Vos, 1972) and *Hesperantha* (Goldblatt, 1984) have a flat side and are bell-shaped.

The nature of the tunics varies considerably and has substantial phylogenetic and taxonomic significance. In subg. *Lapeirousia* the tunics are dark brown, of uniformly woody texture with a smooth surface, and they fragment into irregular pieces with age. The basal margin is ornamented with teeth (cf. Goldblatt, 1972) in sect. *Lapeirousia* (Fig. 1C, E), probably a specialized condition (Goldblatt & Manning, 1990), whereas the margins in sect. *Sophronia* are entire or lightly lobed (Fig. 1D).

In subg. *Paniculata* the tunics range from blackish to pale straw in color and vary in texture from more or less woody to coriaceous. They appear to differ fundamentally from those of subg. *Lapeirousia* in consisting of densely packed fibers

instead of having a uniformly woody texture. Similar textured corm tunics are characteristic of the related genera *Thereianthus* and *Micranthus*, and tunics of densely compacted fibers appear, on the basis of outgroup comparison, to be the basic type for *Lapeirousia* (Goldblatt & Manning, 1990). The way in which the outer layers of the tunics decay in subg. *Paniculata* is often diagnostic. In the five Cape species of subg. *Paniculata* sect. *Fastigiata* (Fig. 1F) the hard, blackish layers fragment rather distinctly into vertical strips that separate from the base (Goldblatt, 1972). A similar pattern is evident in several members of sect. *Paniculata*, such as *L. erythrantha*, *L. rivularis*, and their allies in tropical Africa. The softer-textured tunics of *L. bainesii*, *L. otaviensis*, *L. gracilis*, *L. schimperi*, and *L. coerulea* are assumed to be a specialized condition. These tunics decay with age to form a coarse to sometimes fine reticulum. *Lapeirousia avasmontana*, considered conspecific with *L. coerulea* by Sölch (1969), has distinctive dark brown to blackish tunics that break with age into brittle membranous pieces. The tunics of *L. sandersonii* closely resemble those of *L. avasmontana*, and while the two species have similar divaricately branched panicles with only 1–2 flowers per branch, they nevertheless have such different flowers that it is difficult to believe they are closely related. Their similar corm tunics and inflorescence branching are regarded here as convergent (Fig. 3). The woody tunics of subg. *Lapeirousia* are considered to be a specialized condition in the genus. A few other taxa in Ixioideae have similar woody tunics (*Romulea*, *Syringodea*, *Hesperantha*, *Geissorhiza*), but the corms in these genera are rarely bell-shaped and these genera are generally considered to be only distantly related to *Lapeirousia* (Lewis, 1954; Goldblatt, 1971, 1990a).

CATAPHYLLS

The first foliar organs produced by the sprouting corm, the cataphylls, are entirely sheathing and submembranous. They surround the base of the stem and reach only a few centimeters above the ground. In *Lapeirousia* usually two are produced, and they are often dry and dead at flowering time.

LEAVES

As in most Iridaceae, the foliage leaves of *Lapeirousia* are ensiform and equitant. They are attached to the stem near the base, usually close to ground level (e.g., Fig. 1C), but unlike most genera of Ixioideae, the sheathing leaf bases do not contribute to the corm tunics. This is probably a derived condition (Goldblatt, 1989) shared, in Watsonieae, with *Thereianthus*, *Micranthus*, and *Savannosiphon*, and is important in separating this line from *Watsonia*. The leaves are plane with at least a discrete central vein (pseudomidrib) in subg. *Paniculata* (e.g., Fig. 1B), but are corrugate in subg. *Lapeirousia* (e.g., Fig. 1C). Anatomical differences such as opposed vs. alternate veins and truncate ribs (Table 3) accompany the external differences (Goldblatt & Manning, 1990). In sect. *Paniculata* the leaves are typically narrowly lanceolate, but sometimes are linear (forms of *L. erythrantha*, *L. setifolia*, *L. sandersonii*) or terete (*L. teretifolia*). The leaves of *L. sandersonii* are distinctive in being particularly rigid and fibrotic and in having the several thickened veins set closely together.

STEMS

Stems are usually aerial and branched, and invariably angular to winged, a synapomorphy shared with *Savannosiphon*. While there are subtle differences in the degree of angularity of the stems in different species, the character is not useful taxonomically. In some species of subg. *Lapeirousia* sect. *Sophronia* in southern Africa (Goldblatt, 1972) and in the tropical African *L. odoratissima* (see Fig. 17) the stem is not produced above the ground, and the whole inflorescence is congested into a tufted, rosettelike structure borne at ground level.

INFLORESCENCES

A spicate inflorescence is characteristic of most Ixioideae and is a synapomorphy uniting Watsonieae and Ixieae, two of the three tribes of the subfamily (Goldblatt, 1990a). Most members of subg. *Lapeirousia* have spikes, but in a few species the whole aerial axis is contracted into a cushionlike tuft borne at or near ground level. Among the tropical species of subg. *Lapeirousia*, *L. littoralis* has spikes of 4–12 flowers, these somewhat congested and fewer-flowered in subsp. *littoralis*, and rather lax and with more flowers in subsp. *caudata*. In *L. odoratissima* the aerial stem is contracted and the plant has a tufted appearance (Fig. 17), a habit shared with and perhaps independently evolved in the southern African *L. oreogena*, *L. montana*, and *L. plicata* (Goldblatt & Manning, 1990).

An extensively ramified flowering axis is characteristic of subg. *Paniculata* (Fig. 1A, B), and, although variously called a panicle or corymb, this pseudopaniculate structure is probably a highly ramified spike. Despite sometimes highly developed branching, the ends of the main branches usually carry at least two flowers, and those below the

terminal flower are always sessile and thus arranged exactly like those in the spike of subg. *Lapeirousia* and other Ixioideae with spikes. The pseudopanicle of subg. *Paniculata* is considered a specialized condition in the genus and is the only major synapomorphy for the subgenus (Goldblatt & Manning, 1990).

The degree of inflorescence branching in subg. *Paniculata* is often typical of a species. *Lapeirousia abyssinica* has few-branched stems, and the inflorescence is virtually a branched spike, hardly or not at all different from the branched spikes found elsewhere in Ixioideae. I assume that this is a reversal from the pseudopaniculate condition. In *L. erythrantha* the main branches of the rather lax panicle have 3–5 flowers that tend to be crowded terminally, which impart a corymblike appearance to the sometimes massive inflorescence. The related *L. teretifolia* and *L. angolensis* have only one or two flowers per major inflorescence branch, a feature shared with *L. sandersonii*. *Lapeirousia masukuensis*, which resembles *L. sandersonii* in its long-tubed flowers, has in contrast 5–8 flowers on the terminal branches. Among the long-tubed species of the arid southwest, *L. bainesii* typically has 1(or 2) flowers per main inflorescence branch, whereas *L. otaviensis* and *L. gracilis*, otherwise easily confused with *L. bainesii*, have 3–5 flowers per main branch. Similarly, an important distinction between the easily confused *L. avasmontana* and *L. coerulea* is the number of flowers on the main terminal inflorescence branches, usually 2–4 in *L. avasmontana* and seldom more than one in *L. coerula*.

In subg. *Paniculata* the floral bracts vary little among the species except in size, and they provide limited taxonomic information. However, the bracts are membranous and dry above in sect. *Paniculata*, which outgroup comparison suggests is specialized (Goldblatt & Manning, 1990). In sect. *Fastigiata* the bracts are herbaceous. The bracts are more or less equal in length, but the inner (adaxial) bract is always smaller and is often apically forked or notched. In subg. *Lapeirousia* the bracts are herbaceous and usually have a firm texture, and the inner bracts are shorter than the outer ones. Bract morphology is variable in this predominantly southern African alliance (Goldblatt, 1972), and species can sometimes be recognized by their bracts alone.

FLOWERS

Floral variation is extensive in *Lapeirousia*, as much in tropical as in southern Africa. Two species, *L. coerulea* and *L. avasmontana*, have actinomorphic flowers and short perianth tubes. Their flowers closely resemble those of the SW Cape *L. corymbosa* (sect. *Fastigiata*) and are, I assume, the basic flower type in the genus. The other species of sect. *Paniculata* have zygomorphic flowers with unilateral stamens. The acaulescent *L. odoratissima* also has actinomorphic flowers but has a long perianth tube.

There is considerable variation in perianth tube length in the genus, a feature closely related to the pollination systems of the species and not always indicative of a close phylogenetic relationship. Long tubes of ca. 12–15 cm are found in *L. schimperi* and *L. odoratissima*. A long perianth tube also characterizes *L. littoralis*, in which the degree of variation in length is unusual: subsp. *littoralis* has a tube ca. 28–35 mm long, whereas in subsp. *caudata* the length ranges from 25 to 30 mm in some northern Zambian populations to 50–70 mm in the populations from southern Mozambique. *Lapeirousia bainesii*, *L. otaviensis*, and *L. gracilis*, centered in Namibia, each have similar and relatively long perianth tubes, usually 25–35 mm long. In the *L. erythrantha* complex, *L. masukuensis* and *L. sandersonii* have tubes 15–25 mm long compared with 8–12 mm in other members of the complex, including *L. erythrantha* and *L. setifolia* in which the tube is more or less twice as long as the bracts, a condition that I assume is basal for the alliance. The two tropical species of sect. *Paniculata* with actinomorphic flowers, *L. coerulea* and *L. avasmontana*, have very short perianth tubes, less than 3 mm long, comparable to those in the southern African *L. corymbosa* complex.

The flowers of *Lapeirousia coerulea* and *L. avasmontana* resemble relatively closely those of the southern African actinomorphic-flowered species, and it seems likely in the absence of contrary evidence that the actinomorphic, short-tubed flower with a blue perianth having white markings is basal for the genus (Goldblatt & Manning, 1990). If this is correct, it follows that zygomorphic flowers have evolved independently in subg. *Paniculata* in both the Cape sect. *Fastigiata* and the tropical sect. *Paniculata*, as well as in subg. *Lapeirousia*.

Floral actinomorphy in *Lapeirousia odoratissima* may be secondary, and related to the low stature and tufted habit of this species (Goldblatt & Manning, 1990). I suggested a similar reversal of floral zygomorphy to actinomorphy in the southern African tufted species (Goldblatt, 1972).

The most common perianth form in the zygomorphic species is for the lower three tepals to be

joined for a short distance and displayed horizontally, while the upper tepal is reflexed and held more or less in the same plane as the lower tepals. This is unusual in Ixioideae in which species with zygomorphic flowers usually have the upper tepal held erect or slightly arched over the stamens. The latter type of flower is found in *L. rivularis*, while reflexed tepals are characteristic of all the members of the *L. erythrantha* alliance, including the long-tubed *L. sandersonii* and *L. masukuensis*. The reflexed upper tepal is regarded here as the basal condition, and the erect to arched tepal is considered derived.

The stamens are either erect with filaments contiguous in the actinomorphic-flowered species or unilateral and erect to arcuate in zygomorphic-flowered species. The style follows the orientation of the stamens, and is thus central and erect in species with actinomorphic flowers, and arched behind the stamens in species with zygomorphic flowers. The style branches are divided and recurved for half their length in most species of *Lapeirousia*, and this is assumed to be the basic state for the genus and the tribe Watsonieae. However, several tropical African species of *Lapeirousia* and some forms of the southern African *L. plicata* have undivided style branches. The character is variable within some populations of *L. plicata* and *L. bainesii* that I have examined in the field. It is difficult to assess the significance of this variation, and I have not regarded undivided style branches as having any taxonomic significance.

CAPSULES AND SEEDS

Apart from differences in the size of the capsules and the seeds they contain, fruit characters are of limited use in the taxonomy of *Lapeirousia*. The capsules have firm-membranous walls and range from globose-trigonous to more or less oblong, almost always with the outline of the seeds distorting the outer walls. The seeds are globose to slightly oblong, tapering slightly toward the funicle. The raphal ridge is the only feature distorting the otherwise uniformly microreticulate surface. The seeds are sometimes lightly distorted by pressure. Seed diameter ranges from 2.5 mm in *L. odoratissima* to 1.3–1.8 mm in *L. setifolia*.

Chromosome Cytology

Chromosome number is remarkably variable in tropical African *Lapeirousia* (Goldblatt, 1990b). In sect. *Paniculata* haploid numbers range from $n = 8$ (*L. avasmontana*) to $n = 3$ (one population of *L. bainesii*) (Table 2). Numbers for subg. *Lapeirousia* in southern Africa are $n = 10$, 9, and 8 (Goldblatt, 1972, 1990b). The karyotypes for all species of the subgenus are similar and strongly bimodal, comprising one long chromosome pair and six or seven small pairs less than half as long as the long chromosomes. Of the two tropical species of the subgenus, *L. littoralis* has $n = 7$ and *L. odoratissima*, $n = 8$ and 7.

TABLE 2. Chromosome numbers in tropical African *Lapeirousia* (from Goldblatt, 1990b).

Species	Diploid number $2n$
SUBGENUS *PANICULATA*	
SECTION *PANICULATA*	
L. abyssinica	8
L. angolensis	unknown
L. avasmontana	16
L. bainesii	10, 6
L. coerulea	8
L. erythrantha	12
L. gracilis	12
L. masukuensis	unknown
L. otaviensis	10
L. rivularis	12
L. sandersonii	10
L. schimperi	10
L. setifolia	8
L. teretifolia	unknown
SUBGENUS *LAPEIROUSIA*	
L. littoralis	16
L. odoratissima	16, 18

The Cape species of subg. *Paniculata* have $n = 10$ (Goldblatt, 1972) except *Lapeirousia neglecta* (Goldblatt & Manning, in prep.), which has $n = 5$, and a bimodal karyotype similar to that in subg. *Lapeirousia*. Among the tropical species, *L. avasmontana* has a karyotype most like the Cape members of the subgenus, with one long and seven short pairs in a comparably bimodal karyotype. The species presumably most closely related to *L. avasmontana*, *L. coerulea*, has $n = 4$, now known from seven populations. The karyotype comprises two long and two medium-sized chromosome pairs.

Lapeirousia erythrantha appears to be based on $x = 6$, a number recorded in several populations across its range from southern Malawi to northern Zambia. *Lapeirousia rivularis* also has $n = 6$, but the allied *L. setifolia* and *L. abyssinica* have $n = 4$.

The long-tubed species *Lapeirousia sandersonii*, *L. bainesii*, *L. otaviensis*, and *L. schimperi* appear to be based on $x = 5$. The karyotypes of the last-mentioned three species are similar to each

other, consisting of one particularly long metacentric pair and four shorter pairs, with one metacentric and the other three acrocentric. *Lapeirousia sandersonii* has a more bimodal karyotype with a long, acrocentric pair and four much shorter pairs. While this pattern seems fairly coherent, *L. gracilis*, closely allied to *L. otaviensis*, has $n = 6$ and a bimodal karyotype of one long and five much shorter pairs. Karyotypic variation occurs in *L. bainesii*, one population of the three studied having $n = 3$, with a karyotype of three metacentric chromosome pairs. This pattern suggests Robertsonian fusion of the smaller acrocentric chromosomes of the presumed basic $x = 5$ karyotype of this and related species.

Variability in the karyotypes in *Lapeirousia* is puzzling and difficult to interpret. Elsewhere (Goldblatt, 1990b) I have regarded the bimodal karyotype with $x = 10$ as basic for the genus. It occurs in both subgenera of *Lapeirousia* and in the related *Thereianthus* and *Micranthus*, in which the karyotype is weakly bimodal. This presumes that the lower numbers, $n = 4$ in *L. coerulea*, *L. setifolia*, and *L. abyssinica*, are derived. Judging from the chromosomal variability in *L. bainesii* alone, it seems that the chromosome constitution of *Lapeirousia* is unusually unstable. Structural rearrangement and numerical change may form part of the adaptive strategy of a genus that is remarkable in the family for having radiated in semiarid habitats more severe than those that most genera of Iridaceae favor.

Phylogeny

Within Watsonieae, *Lapeirousia* can be distinguished by its specialized flat-based, bell-shaped corm, the primary synapomorphy for the genus (Goldblatt, 1989; Goldblatt & Manning, 1990). Perhaps most closely allied to *Lapeirousia* (Goldblatt, 1989) is the monotypic *Savannosiphon* (Goldblatt & Marais, 1979), which shares with *Lapeirousia* compressed and angled to winged stems, also a derived condition, and coriaceous to membranous capsules. Except for *Savannosiphon*, which is tropical African, the remaining members of Watsonieae are southern African and are centered in the southwestern Cape. *Thereianthus* and *Micranthus* are endemic to the SW Cape, and *Watsonia* is centered there, although nearly a third of the genus occurs in eastern southern Africa. Within the tribe, *Watsonia* forms one major clade and the *Micranthus–Thereianthus* and *Lapeirousia–Savannosiphon* line form the other (Goldblatt, 1989). This latter clade is defined by having the foliage leaves attached to the stem rather than to the corm, and in having thick, hard-textured tunics composed of compacted fibers. *Thereianthus* and *Micranthus* have an unusual type of seed, appear generally similar, and are almost certainly closely related. *Savannosiphon*, although presumed to be the genus most closely allied to *Lapeirousia*, seems rather different in its broad, soft-textured leaves, unbranched habit, and general appearance, and the possibility that it is misplaced in this scheme cannot be ignored.

Within *Lapeirousia* there are two major species clusters, treated as subgenera by Goldblatt & Manning (1990). Subgenus *Lapeirousia* has specialized corrugate leaves and some associated anatomical specializations (Goldblatt & Manning, 1990), woody corm tunics, and predominantly spicate inflorescences (the latter a symplesiomorphy) (Table 3). Predominantly southern African, the phylogeny of subg. *Lapeirousia* is not considered further here.

Subgenus *Paniculata* has unspecialized plane leaves with a central vein, tunics consisting of densely matted fibers that become ridged, cancellate, or fibrous on aging, two symplesiomorphies, and pseudopaniculate inflorescences and small floral bracts, both derived states. The SW Cape and tropical African members of subg. *Paniculata* appear to comprise separate monophyletic lines, treated as sects. *Fastigiata* and *Paniculata*, respectively (Fig. 3). The largely tropical sect. *Paniculata*, although similar in many ways to sect. *Fastigiata*, can be distinguished by its generally more lax inflorescences and small bracts that are typically dry and membranous above or entirely.

Except for *Lapeirousia coerulea* and *L. avasmontana*, the species of sect. *Paniculata* have zygomorphic flowers, the synapomorphy that unites these 12 species (Fig. 3). In the section, four species form a clade, defined by their long-tubed flowers, pale perianths, and moderately fibrous corm tunics. Of these four species, all except *L. gracilis* have a similar and specialized basic karyotype with $n = 5$ and form a clade within which *L. bainesii* is defined by two synapomorphies: divaricate branching and inflorescence branches with predominantly one flower each; *L. schimperi* is set apart by two synapomorphies: exceptionally long-tubed flowers and a white perianth. I have not identified any synapomorphy for the remaining *L. otaviensis*.

The remaining eight tropical species of sect. *Paniculata* seem related, and they have flowers of similar form, color, and basic markings, yet there is no obvious synapomorphy uniting them. *Lapeirousia sandersonii* and *L. masukuensis* share one synapomorphy, a moderately long perianth tube,

and *L. sandersonii* is further distinguished by its divaricately branched inflorescence with predominantly one- or two-flowered axes and peculiar, smooth corm tunics that fragment into vertical strips. *Lapeirousia avasmontana* shares these two last-mentioned synapomorphies, but its actinomorphic perianth and different karyotype suggest that its similarities with *L. sandersonii* are the result of convergence. *Lapeirousia teretifolia* and *L. angolensis* appear united by their terete leaves.

The remaining species are undoubtedly closely related, but none share notable specializations that indicate that they are more closely allied to one another than to other species in the group. The most notable specialization is in *L. rivularis* in which the upper tepal is erect to hooded instead of being reflexed to lie in the same plane as the lower tepals. This species and *L. erythrantha* are evidently polyploid, $n = 6$, but this may be an independent specialization in each and is so treated here. The possession of the derived chromosome number $n = 4$ in *L. setifolia* and *L. abyssinica* may indicate close relationship, but too few species in the alliance are known chromosomally for this character to be interpreted with confidence. No doubt relationships in this alliance will be better understood when the cytology is better known, but for the present the phylogeny cannot be further resolved objectively.

History of *Lapeirousia*

The first tropical African species of *Lapeirousia*, *L. abyssinica*, was discovered in 1809–1810 by Henry Salt during his East African travels (Salt, 1814), and it had been thoroughly documented in herbaria by 1850 when it was described as a species of *Geissorhiza* (Richard, 1850). In 1878 *G. abyssinica* was transferred to *Lapeirousia*, and the presence of the genus in tropical Africa was thus established (Baker, 1878a). Until then *Lapeirousia* was thought to be an exclusively southern African and largely Cape genus, although *Ovieda erythrantha* from Mozambique had been described in 1864 and transferred to *Lapeirousia* in 1878, at the same time as *L. abyssinica*. The early taxonomic history of *Lapeirousia* and its establishment as a genus thus largely concerns the nontropical species.

Lapeirousia was based on *L. compressa*, described by Pourret in 1788 from a single specimen that was thought to have been collected in Mauritius by the French botanist Philibert Commerson (Goldblatt, 1972). *Lapeirousia compressa* is, however, conspecific with the Cape and Namaqualand endemic, *L. fabricii*, which had been described some 22 years earlier as *Ixia fabricii* by Daniel de la Roche in 1766. The first species of *Lapeirousia* known to science was described 10 years prior to this, when Linnaeus named *Ixia corymbosa*, but the species was only recognized as a member of *Lapeirousia* in 1802. Species of *Lapeirousia* described in the eighteenth century were also placed in *Gladiolus* and *Galaxia*. In 1802, Pourret's *Lapeirousia* was accepted by Ker who transferred the five species of the genus then known to it. Ker also accepted *L. juncea*, which he assigned to the new *Anomatheca* in 1805.

In 1817 Sprengel described *Ovieda*, at first without any species, but in 1825 he placed all the known species of *Lapeirousia*, including by name *L. compressa*, in *Ovieda*, which has the same circumscription as *Lapeirousia* sensu Ker. Renamed *Meristostigma* by Dietrich in 1844 because it was a homonym for *Ovieda* L., *Ovieda* Sprengel nevertheless remained in use, for example by Klatt (1866), until 1876 when J. G. Baker revived *Lapeirousia*.

Sophronia Licht. ex Roemer & Schult. was erected in 1817 for the acaulescent *L. plicata*, but the genus was reduced to a subgenus of *Lapeirousia* by Baker (1892). By then subg. *Sophronia* included three southern African acaulescent species, all now considered conspecific (Goldblatt, 1972). Baker did not, however, regard the acaulescent *L. odoratissima* from tropical Africa as a member of subg. *Sophronia*.

Baker also transferred *Anomatheca* Ker (1805), a genus of five central and southern African species, to *Lapeirousia* as a third subgenus (Baker, 1892). *Anomatheca* is probably most closely related to the southern African *Freesia* (Goldblatt, 1971, 1982), and it has been removed from *Lapeirousia* (Goldblatt, 1972), although Geerinck et al. (1972) treated *A. grandiflora* as a species of *Lapeirousia*. *Freesia* and *Anomatheca* are currently regarded as members of Ixieae, and their deeply divided style branches, shared with *Lapeirousia*, are regarded as a convergent development (Goldblatt, 1990a).

The knowledge of *Lapeirousia* in tropical Africa began to accumulate late in the nineteenth century when Welwitsch's Angolan Iridaceae, collected during 1853–1861 (Rendle, 1899), were studied by Baker (1878b). At this time the widespread *L. schimperi* had already been discovered in Ethiopia by Schimper and referred to *Tritonia* (Klatt, 1866), although it does not have either round-based corms with finely fibrous tunics or the undivided style branches of the latter genus. The same species

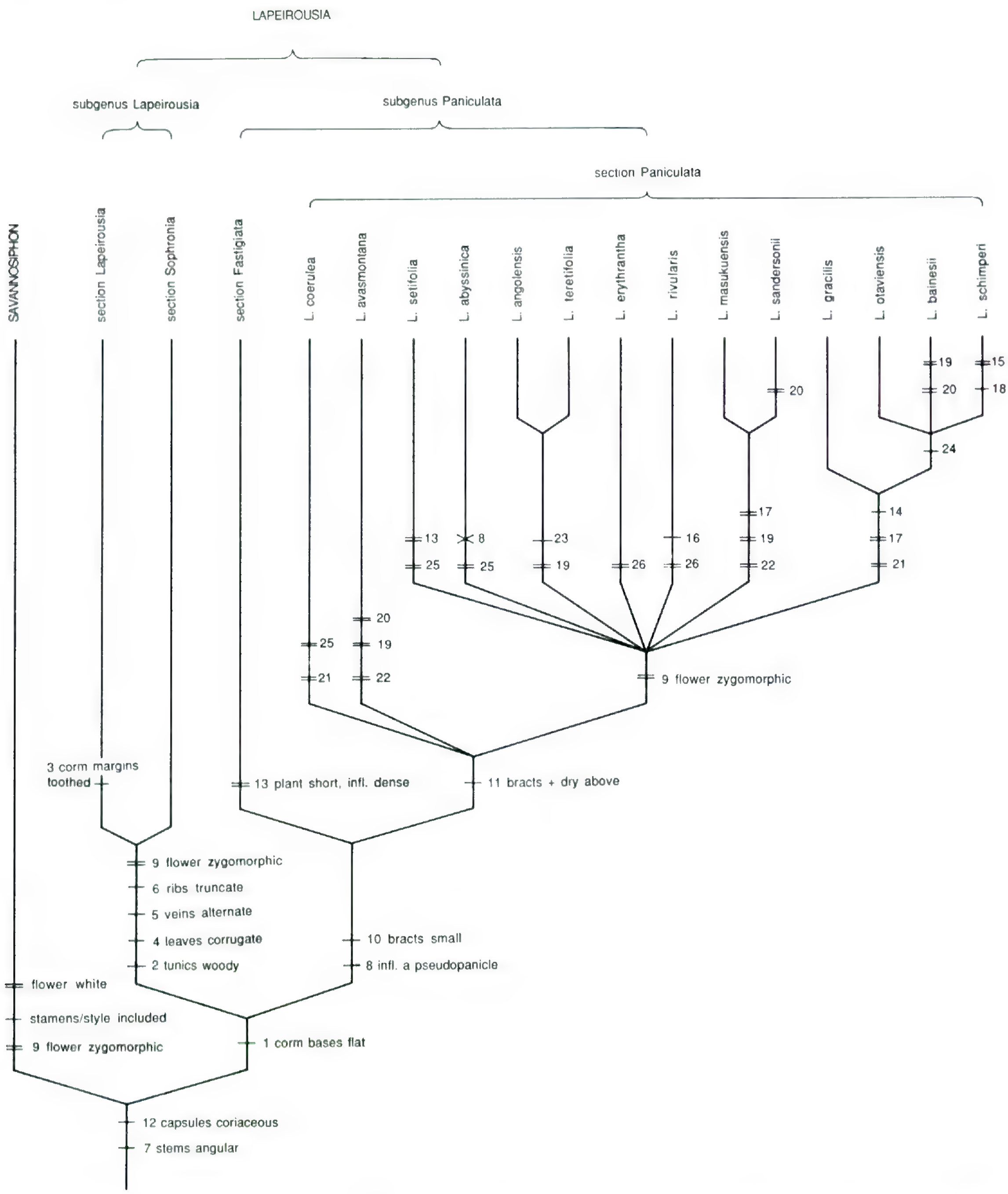

FIGURE 3. Hypothetical phylogeny of *Lapeirousia* showing the major infrageneric lineages and presumed species relationships for sect. *Paniculata*. Characters used in the cladogram are listed in Table 3. Parallelisms are indicated by double horizontal lines and reversals by crossed lines. The cladogram was generated manually: length = 44; consistency index including autapomorphies, CI = 0.64.

collected in Angola was referred by Baker (1876) to *Anomatheca* (*A. monteiroi*), and two more Angolan collections were described as *L. fragrans* and *L. cyanescens*, respectively (Baker, 1878b). *Tritonia schimperi* was transferred to *Acidanthera* (now a synonym of *Gladiolus*) by Baker (1878a), as *A. unicolor*, because its long perianth tube and white flower accorded well with *Acidanthera*. This one species of *Lapeirousia* was thus placed in four different genera over a period of 12 years.

The tropical African species of *Lapeirousia* that occur in the northern Cape and Transvaal were discovered relatively late, with the exception of *L. littoralis*. Although based on an 1859 Welwitsch

TABLE 3. Characters used in the cladogram (Fig. 3). The derived (apomorphic) states are listed first followed by the presumed ancestral (plesiomorphic) conditions. Apomorphies for *Savannosiphon* are taken from Goldblatt (1989). Anatomical specializations for sect. *Fastigiata* known only in one species, *L. corymbosa*, are not included in the cladogram.

1. Corm bases flat—corm bases rounded
2. Corm tunics woody—corm tunics of compacted fibers
3. Margins of corm toothed/spiny—margins of corm not elaborated
4. Leaves corrugate—leaves plane and with a pseudomidrib
5. Major veins alternate—major veins opposite
6. Ribs truncate—ribs rounded
7. Stems angular—stems terete
8. Inflorescence a pseudopanicle—inflorescence a spike
9. Flower zygomorphic—flower actinomorphic
10. Bracts small—bracts relatively large
11. Bracts ± membranous and dry above—bracts herbaceous
12. Capsules coriaceous—capsules woody
13. Plants short and inflorescences congested—plants tall and inflorescences not notably congested
14. Perianth pale-colored—perianth colored blue to purple or red
15. Perianth white without markings—perianth pale or deeply colored, usually with markings
16. Upper tepal erect or hooded—upper tepal recurved and lying in the same plane as the lower
17. Perianth tube 15–40 mm long—tube rarely exceeding 15 mm long
18. Perianth tube 8–12 cm long—tube shorter than 8 cm
19. Branching pattern divaricate—branching ± alternate with a main axis dominant
20. Terminal branches of the inflorescence 1(–2)-flowered—terminal branches with more than 2 flowers
21. Corm tunics becoming fibrous and pale with age—corm tunics remaining relatively densely fibrous and dark-colored
22. Corm tunics smooth and decaying into vertical strips—corm tunics rough, matted, and densely to finely fibrous
23. Leaf terete—leaf plane with midrib evident
24. Base number $x = 5$ (karyotype not bimodal)—karyotype bimodal and $n = 6$ or 5
25. Base number $x = 4$—base number higher
26. Base number $x = 6$ and polyploid—base number different and not polyploid

collection from Angola, *L. littoralis* was actually first collected by William Burchell in 1812 in the northern Cape, but *L. littoralis* had already been described (Baker, 1878b) when Baker named Burchell's plants *L. burchellii* in 1892. The identity of *L. littoralis* has only now been established, the species having previously been known as *L. caudata* subsp. *burchellii* (Goldblatt, 1972). *Lapeirousia caudata*, now *L. littoralis* subsp. *caudata*, was described in 1890 from specimens from northern Namibia. It was based on collections by the Finnish missionary Martti Rautanen and the Swiss botanist Hans Schinz.

The largely Transvaal *L. sandersonii* was first collected by John Sanderson in 1852, but again was named much later by Baker (1892), while *L. bainesii* was first recorded from the remote Kobi Pan in western Botswana by the landscape artist Thomas Baines in 1863 and later found by Emil Holub in 1876 and by Edward Lugard in 1887, also in Botswana. The wide distribution of this species in Namibia was discovered much later, and only in 1942 was *L. bainesii* documented in the Transvaal, where it is rare.

The first east tropical African species of *Lapeirousia* was collected by the German explorer Wilhelm Peters in Mozambique in the mid 1840s. This was the first record of the widespread and common *L. erythrantha*, described by Klatt (1864) as *Ovieda erythrantha*. Later exploration in interior Mozambique and Malawi by John Kirk and David Livingstone soon provided additional records of this species. Its wide distribution and unusual variability led to *L. erythrantha* being given different names in Katanga (*L. briartii* de Wildeman, 1900), Angola (*L. spicigera* Vaupel, 1912), and Zimbabwe (*L. rhodesiana* N. E. Brown, 1911). Rudolf Schlechter's Mozambican collections made in the 1890s yielded additional *L. erythrantha*, although Vaupel (1912) described two as separate species, *L. graminea* and *L. plagiostoma*. At this time Schlechter made the first collections of *L. masukuensis*, also described by Vaupel (1912).

Knowledge of *Lapeirousia* in Namibia was particularly slow to accumulate, owing to difficulties of travel until after the First World War, despite the rich development of the genus there. The common *L. coerulea* as well as *L. otaviensis* were first collected by the Swedish traveler and explorer Ture Een in 1879. These collections were overlooked, and *L. coerulea* was described in 1892 based on later collections, while *L. otaviensis* was named in 1936 by R. C. Foster who based the species on a 1925 collection made by Kurt Dinter. The widespread *L. littoralis* subsp. *caudata* was first collected by Rautanen in 1885 and described as *L. caudata* by Schinz. Later collections of this distinctive subspecies were given different epithets, *L. lacinulata* being described from a Zambian collection, and *L. delagoensis* from specimens from

southern Mozambique. In Namibia the common *L. bainesii* was first collected by Rautanen in 1892, but was not then associated with the Botswanan species. When collected later by Kurt Dinter, it was described as *L. vaupeliana*. Dinter's Namibian collections are particularly important as his several duplicates were distributed to many herbaria. His collections also formed the basis for *L. dinteri* (= *L. schimperi*) and *L. stenoloba* (= *L. littoralis*), described by Vaupel in 1912; *L. avasmontana*, *L. uliginosa* (= *L. schimperi*), *L. juttae* (= *L. odoratissima*), and *L. ramossisima* (= *L. littoralis*), all described by Dinter.

Although Namibia is now fairly well explored botanically, it was only in 1971 that *Lapeirousia rivularis* was described by the Swedish botanist H. E. Wanntorp. The species had been collected as early as 1900 by H. Baum in southern Angola, and by K. H. Barnard in 1921 in northern Namibia but was confused with *L. coerulea* or other species.

Western Zambia and the eastern half of Angola await full botanical exploration, and it is from here that the two new species in this treatment come. Recognized in 1972 as a variety of *Lapeirousia erythrantha* by Geerinck et al., *L. teretifolia* is raised to species rank in this treatment. The new *L. angolensis* is incompletely known and is based on only two collections. Further exploration in Angola is expected to resolve any doubts about this species and should also make it possible to determine the identity of *L. welwitschii*, which was described by Baker (1878b) but cannot be matched satisfactorily with any known species at present owing to the state of the type material. *Lapeirousia bainesii* and *L. otaviensis* are relatively common in northern Namibia but are known from only one or two collections in southern Angola, where they may be fairly common. The establishment of the complete ranges of these species awaits further exploration of this area.

The current circumscription of *Lapeirousia* dates from 1972 (Goldblatt, 1972). In this revision of *Lapeirousia* in the winter-rainfall zone of southern Africa, *Anomatheca* was excluded from *Lapeirousia* and subg. *Sophronia* was not recognized at all. I established two sections for the 19 species treated, sect. *Lapeirousia* including *Sophronia* and sect. *Fastigiata* for the Cape species of what is now recognized as subg. *Paniculata* (Goldblatt & Manning, 1990). The infrageneric classification did not deal at all with the tropical African species, now subg. *Paniculata* sect. *Paniculata*, but recognized the apparently important distinction between corrugate-leafed subg. *Lapeirousia* with woody corm tunics and plane-leafed subg. *Paniculata* with tunics of compressed fibers. The infrageneric classification used here (Goldblatt & Manning, 1990) is a refinement of my earlier classification.

Ethnobotany

As early as 1912 Dinter reported on the use of the corms of *Lapeirousia* species as a food in Namibia. Dinter mentioned specifically that corms of *L. littoralis* (as *L. caudata*), *L. coerulea*, *L. schimperi* (as *L. uliginosa*), and *L. odoratissima* (as *L. juttae*) are a valued food eaten after roasting in hot ashes. Dinter provided vernacular names *onduvi* (*ozonduvi* pl.) (Herero) and *garib* (Khoi) for *Lapeirousia*. Dinter's observation has been confirmed repeatedly by plant collectors and ethnobotanists, notably R. Story for the Kung Bushmen (*L. coerulea*, *Story 6121*, and *L. littoralis*, *Story 6162*).

Rodin (1985) documented that corms of *L. coerulea*, *L. bainesii* (as *L. vaupeliana*), and *L. schimperi* (as *L. cyanescens*) are eaten both raw and roasted by the Kwanyama Ovambos in northern Namibia. The Kung Bushmen are also reported to eat the corms of *L. odoratissima* for their water content (Marshall, 1976). The Kung are reported to bake and eat corms of *L. bainesii* or to pound the cooked corms into a meal, then eat them as a gruel with water (Fox & Young, 1982). In addition, a collection of *L. gracilis* (*Seydel 3419*) documents the edibility of this species.

In light of the amply documented use of the corms of several Namibian species of *Lapeirousia* as food, Watt & Breyer-Brandwijk's (1962) unsubstantiated report that *L. coerulea* is poisonous is doubtful, particularly since their tests performed on a frog for cardiac glycoside action proved negative.

Lapeirousia appears to have little value to human populations outside Namibia and presumably adjacent Angola and Botswana. There are, however, isolated reports that corms of *L. erythrantha* are eaten in the Shire Highlands (southern Malawi) "in time of great famine" (*Buchanan 426*). Collection notes (*Simpathu 60* from Victoria Falls, Zimbabwe) also indicate that corms of *L. erythrantha* are eaten raw.

Systematic Treatment

Lapeirousia Pourret, Mem. Acad. Sci. Toulouse 3: 79–82. 1788. Ker, Konig & Sims, Ann. Bot. 1: 238. 1804. Baker, J. Linn. Soc. Bot.

1: 154–156. 1878; Handbook Irideae 167–174. 1892; Fl. Capensis 6: 88–97. 1986; Fl. Tropical Africa 7: 350–355. 1898, excluding subg. *Anomatheca*. Sölch, Prod. Fl. Südwestafrika 155: 6–10. 1969. Goldblatt, Ann. Bolus Herb. 4: 14–74. 1972. Geerinck, Bull. Soc. Roy. Bot. Belgique 105: 333–351. 1972.

For the generic synonymy see Goldblatt (1972).

Plants perennial geophytes, deciduous in the dry season. *Rootstock* a bell-shaped corm with a flat base, the tunics hard-textured, woody to coriaceous, entire and concentric initially, becoming irregularly fragmented with age, or composed of compressed fibers and then becoming cancellate to loosely fibrous with age. *Cataphylls* usually 2, membranous, the inner one reaching shortly above the ground, the outer about half as long, pale to partly brown or uniformly dark brown. *Leaves* 2–several, often only 1 inserted at the base near ground level and this largest, sheathing below, blade isobilateral for the most part but often channeled above the sheath for a short distance or up to half its length, other leaves sometimes basal or more often inserted aboveground and progressively shorter above, linear to lanceolate with a plane surface and a central vein evident, sometimes terete to oval in section (subg. *Paniculata*), or corrugate and the central vein no more prominent than the other veins (subg. *Lapeirousia*). *Stem* erect, somewhat compressed and 2–3-angled, often more conspicuously so above, the angles often weakly winged. *Inflorescence* paniclelike or a simple to branched spike, the panicles often somewhat corymbose; individual flowers always with a pair of opposed bracts at the base of the ovary; *bracts* herbaceous to membranous, the outer abaxial and often the largest, sometimes ridged or keeled, the keel sometimes crisped or toothed (subg. *Lapeirousia*); the inner bract adaxial, usually with 2 veins, and frequently bifurcate. *Flowers* actinomorphic or zygomorphic, the perianth petaloid, often brightly colored, forming a short to extended tube, the tepals subequal or unequal, then usually with the upper tepal largest and the lower 3 smallest and forming a lip and provided with nectar guides of contrasting coloration. *Stamens* symmetrically disposed or unilateral and erect to arcuate; *filaments* filiform, inserted below the mouth of the tube; *anthers* oblong to linear, longitudinally dehiscent, sub-basifixed to nearly centrifixed. *Ovary* globose to ovoid, concealed by the bracts; *style* filiform, dividing into 3 above, the branches usually forked for up to half their length, occasionally entire or barely bifid. *Capsules* membranous to coriaceous, globose to 3-lobed; *seeds* ± globose to weakly angled by pressure, the surface rough. *Haploid chromosome numbers* $n = 10, 9, 8, 7, 6, 5, 4, 3$, the karyotypes often bimodal. TYPE SPECIES: *Lapeirousia compressa* Pourret (= *L. fabricii* (de la Roche) Ker).

Named by French naturalist Abbé Pierre André Pourret (1754–1818) in honor of his colleague and contemporary, Philippe Picot de Lapeirouse, botanist and mineralogist at the University of Toulouse. The first and only species to be so named was thought by Pourret to have come from Isle de France (Mauritius). Had Pourret known that it was a Cape species he probably would have placed it in *Gladiolus* or *Ixia*, genera to which other species of *Lapeirousia* were at that time assigned.

KEY TO *LAPEIROUSIA* IN TROPICAL AFRICA INCLUDING BOTSWANA, NAMIBIA, AND TRANSVAAL, SOUTH AFRICA

* Species marked with an asterisk are predominantly southern African and restricted to southern Namibia, largely to the southwestern corner that receives winter rainfall. They are treated fully by Goldblatt (1972).

1a. Axis contracted above ground level, the inflorescence congested and plants tufted in appearance; floral bracts herbaceous and hardly different from the leaves.
  2a. Floral bracts 6–15 cm long; perianth tube 10–14 cm long ..... 16. *L. odoratissima*
  2b. Floral bracts 4–5 cm long; perianth tube ca. 3.5 cm long ..... *L. plicata**
1b. Axis including the inflorescence extending above the ground and relatively lax; floral bracts herbaceous to ± membranous and dry but unlike the foliage leaves.
  3a. Perianth tube (2–)2.5–15 cm long (if less than 2.5 cm then the tepals narrower than 2 mm).
    4a. Perianth tube 10–15 cm long; tepals 6–7 mm wide ..... 14. *L. schimperi*
    4b. Perianth tube 2–7 cm long; tepals 1.5–5 mm wide.
      5a. Tepals at least 15(–30) mm long; flowers shades of white to cream, rarely purple, with or without markings on the lower tepals.
        6a. Tepals 1.3–3 mm at the widest; flowers without markings on the lower tepals ..... 15. *L. littoralis*
        6b. Tepals 4–5 mm at the widest; flowers with violet markings on lower tepals ..... 12. *L. otaviensis*

5b. Tepals 8–14 mm long; flowers shades of blue to violet, sometimes white to cream, or greenish, but always with contrasting markings on the lower three tepals.
7a. Inflorescence a divaricately branched panicle with the main branches 1(or 2)-flowered.
8a. Perianth white to pale pink; corm tunics straw-colored and ± fibrous and reticulate; perianth tube 25–34(–40) mm long, rarely shorter ..... 13. *L. bainesii*
8b. Perianth blue to violet; corm tunics dark brown, consisting of irregularly broken strips; perianth tube 15–18(–20) mm ..... 10. *L. sandersonii*
7b. Inflorescence a panicle or spike with at least some main branches 3–8-flowered.
9a. Perianth greenish or blue-violet with red to purple markings on the lower tepals; plants of Mozambique, Transvaal, and Zimbabwe ..... 9. *L. masukuensis*
9b. Perianth white or pale blue with bluish markings on the lower tepals; plants of Namibia ..... 11. *L. gracilis*

3b. Perianth tube 1–20(–25) mm long (if 20–25 mm then the tepals at least 2 mm wide).
10a. Perianth tube shorter than 2 mm; flower actinomorphic.
11a. Flowers 1(or 2) on terminal branches of the inflorescence; tepals 11–15.5 mm long; corm tunics dark brown to blackish and decaying irregularly into vertical strips ..... 2. *L. avasmontana*
11b. Flowers (2–)3–5 on terminal branches of the inflorescence; tepals 7–9.5 mm long; corm tunics light brown and forming a fibrous network ..... 1. *L. coerulea*
10b. Perianth tube 3–20(–25) mm long; flower medianly zygomorphic with arcuate unilateral stamens.
12a. Leaves corrugate and without an evident main vein; floral bracts herbaceous, usually longer than 16 mm, and the outer bract much longer than the inner; South Africa and southern Namibia.
13a. Perianth tube with the throat much wider than the lower part ..... *L. dolomitica**
13b. Perianth tube slender and ± uniform throughout ..... *L. barklyi**
12b. Leaves either plane and with an evident midvein (at least when living) or rounded to terete and the midrib then not evident, but not corrugate; floral bracts herbaceous to membranous, usually shorter than 10 mm and the outer bract about as long or shorter than the inner; Transvaal, Namibia, and tropical Africa.
14a. Perianth tube 15–20(–25) mm long.
15a. Main inflorescence branches 1(or 2)-flowered; leaves 1–3 mm wide; branching ± divaricate ..... 10. *L. sandersonii*
15b. Main inflorescence branches 5–8-flowered; leaves 3–6 mm wide; branching unequal with the main axis straight ..... 9. *L. masukuensis*
14b. Perianth tube 8–12(–15) mm long.
16a. Inflorescence a simple or branched spike with rarely more than 2 lateral branches; bracts 6–8(–10) mm long; plants seldom exceeding 20 cm high; plants of northern Ethiopia and eastern Sudan ..... 8. *L. abyssinica*
16b. Inflorescence a panicle or several-branched spike (rarely with fewer than 3 lateral branches); bracts 5–6 mm long; plants often taller than 20 cm; plants of Nigeria or south tropical Africa, including Botswana and Namibia.
17a. Inflorescence a lax panicle with the main terminal branches mostly 3–5-flowered; upper tepal suberect to curving forward over the stamens ..... 3. *L. rivularis*
17b. Inflorescence a lax to dense panicle with the main terminal branches 1–5-flowered; upper tepal erect to patent, spreading outward, thus not hooded over the stamens.
18a. Leaves narrow, 1–1.5 mm diam., elliptic to terete in section and without an evident midrib; perianth tube 3–5 mm long and tepals 5–14 mm long; main inflorescence branches with 1 or 2 flowers.
19a. Perianth tube exceeding the bracts by 2–3 mm and only slightly shorter than the tepals; tepals 5–6 mm long ..... 6. *L. teretifolia*
19b. Perianth tube barely exceeding the bracts and less than half as long as the tepals; tepals 12–14 mm long ..... 7. *L. angolensis*
18b. Leaves plane, narrow to broad, 0.5–8(–11) mm wide and always with a defined midrib; perianth tube 7–14 mm long and tepals 7–11 mm long; at least some inflorescence branches with more than 2(–8) flowers.
20a. Plants rarely taller than 12 cm; bracts herbaceous at anthesis; branching usually contorted ..... 5. *L. setifolia*
20b. Plants (15–)20–45 cm high; bracts generally membranous and dry above at anthesis; branching not contorted ..... 4. *L. erythrantha*

For the southern African countries of Botswana, Namibia, and South Africa, cited specimens are arranged according to the grid reference system based on geographical degree coordinates of latitude and longitude currently used in floristic treatments for the subcontinent (Edwards & Leistner, 1971). All type material cited was seen unless otherwise indicated.

Descriptions are based on both fresh and the available dried material, but measurements are based on living plants whenever possible. A shrinkage factor of 20% or more may be expected for flower parts, and 10% for leaves, depending on the care and method of preservation. Flower color fades progressively in dry specimens, eventually changing completely, becoming darker or lighter and sometimes ultimately disappearing. Color notes on collected specimens are desirable and are frequently mentioned by collectors.

SUBGENUS *PANICULATA* GOLDBL. & MANNING
SECTION *PANICULATA*

1. Lapeirousia coerulea Schinz, Verh. Bot. Verein. Brandenburg 31: 212–213. 1890. Baker, Handbk. Irideae 168. 1892; Fl. Trop. Africa 7: 351. 1898. Sölch, Prod. Fl. Südwestafrika 155: 8–9. 1969 (including *L. avasmontana*). TYPE: Namibia, (Upingtonia) Ombale, südost Ondonga, Mar. 1886, *Schinz 13* (lectotype, K, here designated; isolectotype, COI); Hereroland, *Lüderitz 28* (syntypes, B, Z); Otjitambi im Kaoko, *Belck 50* (syntype, not seen). Figure 4.

Ixia dinteri Schinz, Mém. Herb. Boissier 20: 14. 1900. TYPE: Namibia: Karibib, Spitzkop, marshy ground, *Dinter 22* (*32* on the type) in 1898 (holotype, Z).

Plants (12–)15–30 cm high, branched repeatedly. *Corm* 12–16 mm diam. at the base, light brown, the tunics of pale compacted fibers decaying to become coarsely to finely fibrous and reticulate. *Cataphylls* 2, pale to light brown. *Leaves* 2–4, only the lowermost inserted at the base, this leaf longest and reaching to the middle of the inflorescence or beyond, ± linear, 2–4(–5) mm wide, the upper leaves decreasing in size above. *Stem* compressed, 2–3-angled, often intricately branched. *Inflorescence* a lax panicle with ascending branches, the larger terminal branches bearing (2–)3–5 sessile flowers; *bracts* 3–4 mm long, herbaceous below, membranous apically and becoming completely dry in fruit, the inner bracts about as long as the outer. *Flower* actinomorphic, ± stellate, blue to light purple with a white hastate marking outlined in dark blue to violet (less often reddish) in the lower half of each tepal; *perianth tube* 1–1.5 mm long, cylindric below, widening above, the cylindric part shorter than 1 mm; *tepals* spreading below, curving upward distally, subequal, lanceolate, 7–9.5 mm long, 3–5 mm wide. *Filaments* inserted below the mouth of the tube, united basally for less than 0.5 mm by an obscure coronalike ring, erect, ca. 4 mm long, nearly contiguous around the style; *anthers* diverging, 3–3.5 mm long, curving inward after anthesis; pollen light blue-purple (white to yellow when dry). *Ovary* ca. 2 mm long, *style* erect, 6–7 mm long, dividing near the anther apices, branches ca. 1.2 mm long, barely notched apically. *Capsules* obovoid-globose, weakly 3-lobed, ca. 4 mm long; *seeds* dark brown, globose to weakly angled by pressure, 1.3–2 mm diam., tapering near the attached funicle. *Chromosome number* $2n = 8$.

Flowering time. (January)February to April.

Distribution and habitat. Typically a species of damp, low-lying places, *Lapeirousia coerulea* is widespread throughout the summer-rainfall part of Namibia (Fig. 4) where it occurs in seeps, seasonal vleis, damp poorly drained grassland, and shallow soil in rock outcrops where water accumulates in the wet season. There are a few records from northwestern Botswana, where it is apparently rare.

Several collections are accompanied by notes indicating that *Lapeirousia coerulea* is eaten by natives, particularly the Kung Bushmen for whom the corms are a staple, eaten after roasting in hot ash (*Story 6121*), or sometimes raw (Rodin, 1985).

Diagnosis and relationships. Lapeirousia coerulea and the closely allied *L. avasmontana* appear to be taxonomically isolated among the tropical African members of the genus in their short-tubed and completely actinomorphic flowers. However, their paniculate inflorescences indicate a relationship with the tropical African sect. *Paniculatae*. The actinomorphic, blue flowers with their vestigial perianth tube and unusually short, undivided style branches make the two species easy to recognize. The differences between *L. coerulea*, a species of wet low-lying places, and *L. avasmontana*, which grows in well-drained stony banks and hills (discussed in detail under *L. avasmontana*), involve vegetative and floral features, including corm tunics, branching pattern of the inflorescence, and flower size and patterning. These morphological differences, combined with the disparate

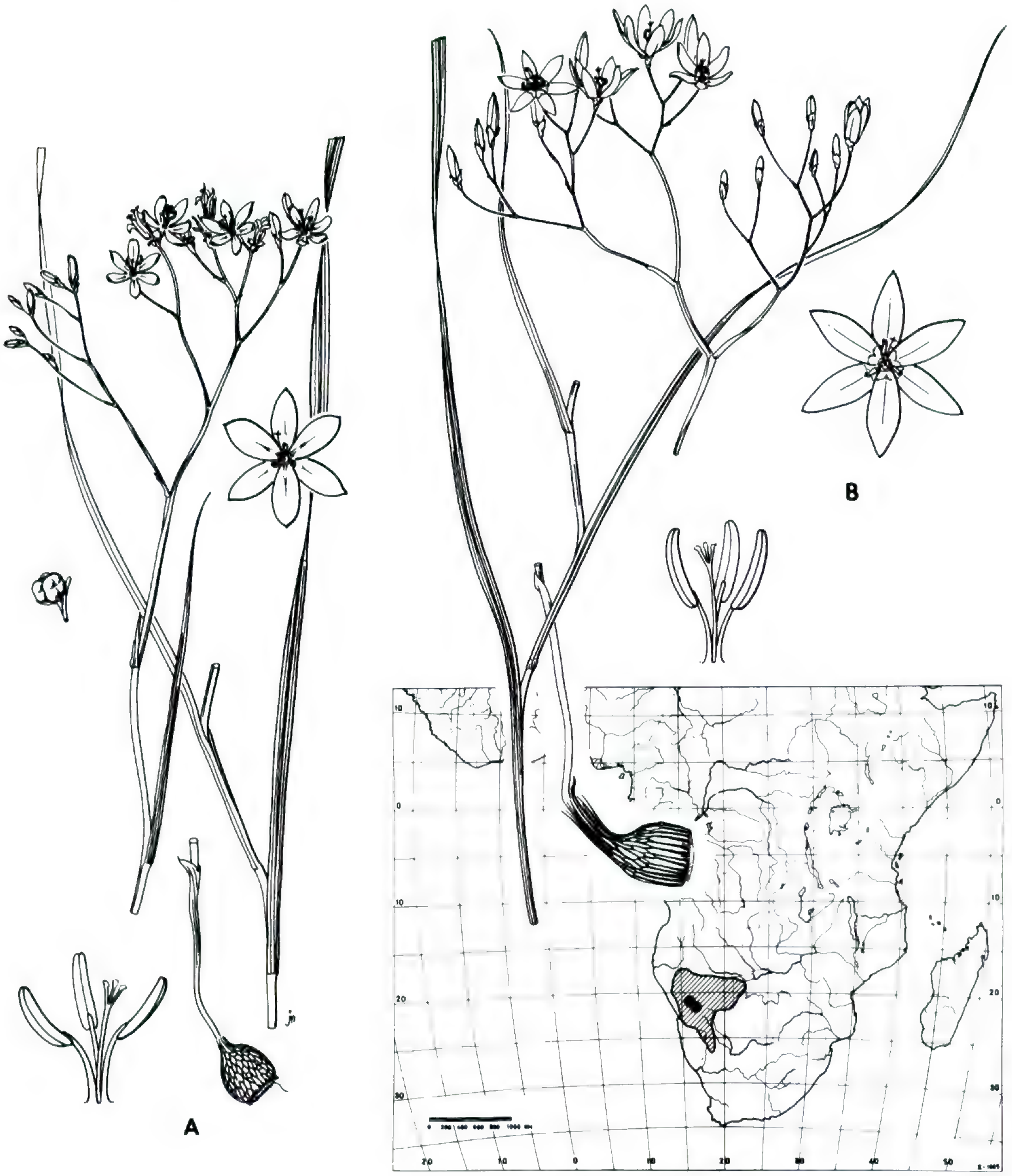

FIGURE 4. Morphology and distribution of *Lapeirousia coerulea* (A) (and hatched area) and *L. avasmontana* (B) (and closed circles). Habits and corms × 0.5; single flowers and fruit full size; details of stamens and style × 2. (Drawn by J. C. Manning.)

habitat preferences and karyotypes (discussed below), compel their separation even though Sölch (1969) united them.

A diploid number of $2n = 8$ has been recorded in seven populations of *Lapeirousia coerulea* (Goldblatt, 1990b). The karyotype consists of two larger and two smaller chromosome pairs. This low and apparently derived number also occurs in the Ethiopian *L. abyssinica* and in *L. setifolia*, both of which have karyotypes comparable to but somewhat different from that of *L. coerulea*. *Lapeirousia avasmontana* has $2n = 16$, but it is clearly not a direct polyploid derived from ancestors such as *L. coerulea*. Its karyotype comprises one long and seven short chromosome pairs, and it has about the same amount of chromosome material per cell as *L. coerulea*. Base number in *L. coerulea* is consistent with its placement in sect. *Paniculatae*. Despite its actinomorphic flowers, *L. coerulea* is probably most closely related to the *L. erythrantha*

group of species, all of which have longer-tubed, zygomorphic flowers. Chromosome numbers in the section are $2n = 12$, 10, 8, and 6 (Goldblatt, 1990b), and the karyotypes in the group are weakly, if at all, bimodal. The simple flower structure of *L. coerulea* makes it appear to be close to the basal stock of the tropical African species.

History. The widespread *Lapeirousia coerulea* was first collected in 1879 by the Swedish traveler and explorer Ture Een on his second major expedition to Namibia. This early record received no attention, and collections made after 1885 independently by Hans Schinz, August Lüderitz, and Waldemar Belck formed the basis for the protologue published by Schinz in 1890. In 1900 Schinz also described *Ixia dinteri*, a species undoubtedly conspecific with *L. coerulea*, based on specimens collected by Kurt Dinter in 1898.

Additional specimens examined. BOTSWANA. NGAMILAND: 19.21 (Aha Hills) Xangwe, Mar. 1961 (CB), *Gibson 186* (MO, WIND); Dobe region, north of Aha Hills near Namibian border, dry pan, 25 Apr. 1980, *Smith 3496* (MO, PRE, SRGH); Dobe, 19 Sep. 1964, *Lee 13* (SRGH); hard clay in dry pan, Quangwa River catchment, 19°35″ 21°2″, 23 Apr. 1981, *Smith 3674* (BR, PRE). GHANZI: 21.22 (Kobe) pan on farm 102, Kuki, 21 Feb. 1970 (AC), *Brown & Brown 8723* (C, PRE, SRGH); 53 km NE of Ghanzi on the road to Maun, 22°05″ 21°26″, seasonally flooded limestone outcrops, 29 Dec. 1977, *Skarpe 213* (K, MO, PRE, UCBG). NAMIBIA. OVAMBOLAND: 17.15 (Ondangua) 3 km S of Oshikango, 3 Apr. 1973 (BD), *Rodin 9203* (K, M, MO, PRE, WIND). ETOSHA: 18.15 (Okahakana) Etosha Pan, large vlei 5 mi. W of Okondeka, 27 Mar. 1963 (DD), *Giess et al. 6056* (M, WIND); NW Ecke des Etosha National Park, trockene randzone von vlei, 18 Mar. 1974, *Mermüller & Giess 30378* (M, PRE). GROOTFONTEIN: 19.17 (Tsumeb) 25 km from Tsumeb toward Ondangua, 14 Feb. 1983 (BA), *Lavranos & Pehlemann 21101* (WIND); farm Toevlug, lime marl, 5 Feb. 1971, *Giess 11292* (K, MO, PRE, SRGH, WAG, WIND); farm Goab, spring meadows, 29 Jan. 1978 (CA), *Giess 14955* (M, MO, PRE, WAG, WIND); 19.18 (Grootfontein) Grootfontein, red loamy flats (CA), Jan. 1935, *Schoenfelder 35* (K, PRE); 13 mi. N of Grootfontein, 14 Jan. 1934, *Schoenfelder 434* (PRE); farm Kumkaus (GR 552), in vlei, 7 Mar. 1974, *Merxmüller & Giess 30107* (M). OKAVANGO: 19.20 (Tsumkwe) pans at Tsumkwe, 14 Jan. 1971 (DA), *Giess et al. 11076* (M, S, PRE, WIND); Tsumkwe, 14 Jan. 1958, *Story 6121* (M, PRE, SRGH). OUTJO: 22.15 (Otjihorongo) farm Goreis, red loam sand, 17 Feb. 1971 (BB), *Giess 11248A* (K, M, PRE, WIND). OTJIWARONGO: 20.16 (Otjiwarongo) Otjiwarongo (BC), s.d., *Barnard 198* (SAM); 30 km S of Otjiwarongo, 1985 (CB), *Lavranos 22698* (MO); 20.17 (Waterberg) omuramba at Omam, 11 Mar. 1940 (CA), *Volk 2845* (WIND). GOBABIS: 21.18 (Steinhausen) farm Wilhelmsruhe, 10 Feb. 1982 (DC), *Rauh 57762* (WIND). WINDHOEK: 22.17 (Windhoek) Neudam Experimental Farm, 22 Mar. 1960 (AD), *van Vuuren 1027* (K, M, PRE, SRGH, WIND); Ongombo, N of Neudamm, 26 Dec. 1963, *Giess 243* (M); farm Otjikundua 67 mi. WSW of Steinhausen, open vlei, 19 Feb. 1955 (BA), *de Winter 2409* (K, M, NBG, PRE, WIND); farm Aris, S of Windhoek, omuramba, 1 Mar. 1953 (CA), *Walter & Walter 1550* (B, BR, WIND). OMARURU: 21.15 (Karibib) Ohere-Oos, granite flats, 14 Feb. 1958 (BA), *Merxmüller & Giess 1583* (M, PRE, WIND); 30 km NW Omaruru, 19 Apr. 1968, *Wanntorp 805* (K, S). KARIBIB: 21.15 (Karibib) Ameib Ranch, granite rock flushes at Bull Parties, 15 Mar. 1988 (DC), *Goldblatt & Manning 8811A* (M, MO, PRE, WAG, WIND); 22.15 (Trekkopje) Okongawa, Granitbankberg, 4 Feb. 1934 (BB), *Dinter 6957* (B, BOL, G, K, HBG, M, PRE, S, WIND, Z). OKAHANDJA: 21.16 (Okahandja) farm Omatako View, 15 Feb. 1974 (BA), *Woortman 116* (M, PRE, WIND); farm Omongongua, shallow depressions in omuramba, 27 Mar. 1960 (DB), *Seydel 2203* (B, K, GH, MO, WIND); farm Omungongua, Okahandja, 1953, *Walter & Walter 1510* (B, K); farm Okambahe, ca. 16 mi. W of Okahandja on the road to Karibib, 21 Dec. 1963 (DC), *Giess et al. 5058* (M, MO, PRE, WIND). REHOBOTH: 23.16 (Nauchas) farm Göllschau, 27 Jan. 1972 (BC), *Giess & Hübsch 11600* (M, PRE, WIND); 23.17 (Rehoboth) farm Gravenstein, 20 Nov. 1956 (BC), *Volk 11503* (M, MO, WIND); farm Tsumis, sandy soil (CA), *Müller 1396* (M, PRE, WIND). KEETMANSHOOP: 26.18 (Keetmanshoop) Spitzkoppe, 7 Apr. 1984 (AD), *Craven 1533* (WIND). WITHOUT PRECISE LOCALITY: NAMIBIA: Damaraland, 1879, *Een s.n.* (BM); Otavital, 26 Feb. 1925, *Dinter 5663* (B, GH, Z); Kalahari, 1886, *Ross s.n.* ex Herb. Schinz (M); farm Schoengelegen, 22 Feb. 1961, *Seydel 2609* (BR, COI, M, MO, WAG).

2. Lapeirousia avasmontana Dinter, Feddes Rep. 29: 256. 1931. TYPE: Namibia: Lichtenstein, Auas Mountains, 20 Feb. 1923, *Dinter 4454* (holotype, B; isotypes, GH, K (photo), S, Z (3)). Figure 4.

Plants 20–30 cm high, branched repeatedly. *Corm* 15–20 mm at the widest diam., tunics dark brown to blackish, the inner layers ± woody, the outer decaying irregularly, often into vertical strands. *Cataphylls* 2, membranous, usually brownish, the inner one reaching shortly above the ground. *Leaves* 3–4, linear, 2–3 mm wide, only the midrib prominent, the lowermost leaves inserted near ground level and longest, usually slightly longer than the inflorescence, other leaves inserted above the ground and progressively smaller above, those subtending branches becoming bractlike. *Stem* ± divaricately branched above, rounded to lightly triangular, sometimes obscurely winged or ridged at one or more of the angles. *Inflorescence* a rounded corymbose panicle, the ultimate branches with 1(or 2) flowers; *bracts* 5–6 mm long, herbaceous below, membranous in the upper half and bent outward by the tepals, becoming completely dry in fruit, the inner bract about as long or longer than the outer. *Flower* actinomorphic, blue to light purple with a white heart-shaped mark feathered purple on the edges in the lower midline of each tepal; *perianth tube* ca. 1 mm long, cylindric in the lower

half, widening above; *tepals* spreading outward and curving upward apically, subequal, lanceolate to elliptic, 11–15.5 mm long, (4–)5–7 mm wide. *Filaments* inserted at top of the slender part of the tube, erect, 4–5 mm long, in the lower half nearly contiguous around the style, diverging above; *anthers* diverging, 4–5 mm long, curving inward after anthesis; pollen light blue-purple to whitish. *Ovary* ca. 2 mm long; *style* erect, 6–7 mm long, dividing near the anther apices, branches ca. 1.2 mm long, barely notched apically. *Capsules* ± globose, weakly 3-lobed, showing the outline of the seeds, 6–8 mm long, ca. 7 mm diam.; *seeds* globose, dark brown, 1.5–2 mm diam., rounded to weakly angled by pressure, tapering toward the attached funicle. *Chromosome number* $2n = 16$.

Flowering time. February to April.

Distribution and habitat. *Lapeirousia avasmontana* is endemic to central interior Namibia, where it is locally common on the hills and mountains around Windhoek and in the north toward Okahandja (Fig. 4). Apparently preferring well-drained sites, it grows on open, stony, sloping ground. Depending on the rainfall, flowering may last between three and eight weeks. New branches continue to be produced from the cauline leaf axils as long as the ground remains moist, and a late rainfall can stimulate production of a second flush of flowering from new branches on the same flowering stem. The bright blue flowers are visited by a variety of insects including bees, wasps, and butterflies. No measurable nectar is produced, and presumably the only reward to insect visitors is pollen. The very short perianth tube and blue, stellate flower suggest that the species, like the morphologically similar *L. coerulea*, depends on short-tongued pollen-foraging bees for pollen transfer.

Diagnosis and relationships. The large, pale blue (blue-lilac) flowers with a white center, completely actinomorphic perianth and stamens, and large umbrellalike, paniculate inflorescence distinguish *Lapeirousia avasmontana* from other tropical and subtropical African species of the genus. It is most easily confused with the more widespread Namibian species *L. coerulea*, which has similar but smaller actinomorphic flowers. *Lapeirousia avasmontana* has dark brown, more or less woody corm tunics that break into vertical strips as they decay and a divaricately branched inflorescence, the terminal branches of which bear a single (rarely two) flowers. Both features contrast strongly with *L. coerulea*, which has light brown tunics that become fibrous and reticulate as they decay, and a less strongly branched inflorescence of ascending branches, some of which terminate in spikes of 3–5 flowers. The flowers of the two species also differ, those of *L. avasmontana* having somewhat larger, pale blue tepals 11–15.5 mm long, with heart-shaped white markings, compared with those of *L. coerulea* having tepals 8–9 mm long, with hastate white markings. These differences were noted in the protologue by Dinter (1931), who was aware of the possible confusion between *L. avasmontana* and *L. coerulea*.

Chromosome cytology provides additional information about the status of *Lapeirousia avasmontana*. Its diploid chromosome number is $2n = 16$, and the strongly bimodal karyotype consists of 2 long and 14 short chromosomes (Goldblatt, 1990b). *Lapeirousia coerulea* has, in contrast, $2n = 8$ and a karyotype of four long and four shorter chromosomes. Despite the apparent numerical polyploid relationship, their karyotypes differ so much that it is clear that a more complex situation is involved. Karyology supports the separation of the two species and suggests that they are not particularly closely related.

History. *Lapeirousia avasmontana* was discovered in 1923 by Kurt Dinter who described it in 1931. In the protologue *Lapeirousia avasmontana* was compared closely with the similar *L. coerulea* which, as Dinter pointed out, grows in a different habitat and differs in the several vegetative and floral morphological features mentioned above. Although *L. avasmontana* was included in *L. coerulea* in the *Prodomus Flora Südwestafrika* (Sölch, 1969), I have no hesitation in recognizing it as a separate species.

Additional specimens examined. NAMIBIA. WINDHOEK: 22.16 (Otjimbingwe) farm Onduno, Hochflaeche, 27 Feb. 1966 (BD), *Meyer 115* (MO, WIND); farm Terra Rossa, rocky slope, 13 May 1973 (CD), *Giess 13498* (K, M, NBG, PRE, WAG, WIND); farm Friedenau, 25 Mar. 1982 (DB), *Müller & Kolberg 2039* (PRE, WIND); 16 Apr. 1939 (fl & fr), *Gassner 134* (M); 22.17 (Windhoek) Elisenheim, Erosberge, below Wächter, smooth shale slopes, 28 Feb. 1974 (AC), *Merxmüller & Giess 30017* (K, M, S, PRE, SRGH, WAG, WIND); near Brakwater on the Windhoek-Okahandja road, 14 Mar. 1959, *de Winter & Giess 7136* (M, PRE, WIND); Auasberge near Windhoek, Moltkeblick, 24 Mar. 1969 (CA), *Meyer* sub *Giess 10725* (WIND); 5 km W of Windhoek on Daan Viljoen road, stony quartz hill slopes, 14 Mar. 1988, *Goldblatt & Manning 8798* (E, K, M, MO, NBG, PRE, S, WAG, WIND).

3. Lapeirousia rivularis Wanntorp, Svensk. Bot. Tidskr. 65: 53–56. 1971. Roessler &

Merxmüller, Mitt. Bot. Staatssamml. München 15: 394–395. 1979. TYPE: Namibia: Karibib, farm Ameib, ca. 25 km NE of Usakos, granite kopje S of track, ca. 5 km E of farmhouse, 15 Apr. 1968, *Wanntorp & Wanntorp 907* (holotype, S; isotype, M). Figure 5.

Plants 30–45 cm high, paniculately branched. *Corm* 12–22 mm wide at the base, tunics dark brown to blackish, coarsely fibrous or cancellate. *Cataphylls* 2, membranous, pale to dark brown, the inner one reaching shortly above the ground. *Leaves* 3–5, the lower 2 ± basal, bifacial and channeled for at least half their length, reaching to about the base of the inflorescence, linear and unifacial above, 2–3 mm wide, firm-textured, midrib lightly raised, the upper leaves subtending the branches of the inflorescence, bifacial for all or most of their length, progressively shorter above. *Stem* weakly compressed and 3–4-angled, usually laxly branched. *Inflorescence* a rounded to elongate panicle, the ultimate branches bearing (1–)3–5 flowers, laxly arranged; *bracts* 4–6(–9) mm long, green below, membranous and reddish in the upper half, apically dry and brown-tipped in bud, later becoming dry for ⅔ of their length, inner bract about as long as the outer and entire or apically forked. *Flower* zygomorphic, pale blue-mauve with white to cream nectar guides on the lower 3 tepals outlined in deep violet, sometimes with a median red streak, the reverse of the tube bluish; *perianth tube* ascending, narrowly funnel-shaped, ca. 1.3 mm wide at the base, 3 mm at the mouth, 7–9 mm long, weakly curved in the upper third; *tepals* lanceolate, subequal in size, (7–)10–13 mm long, 4–5 mm wide, the margins somewhat undulate, the upper tepal suberect to arching over the stamens, others directed forward, the lower 3 nearly horizontal, joined for ca. 1 mm longer than the upper, sometimes each with an obscure to conspicuous bump or callus in the median lower half. *Filaments* unilateral and arcuate, 8.5 mm long, inserted 3–4 mm below the mouth of the tube; *anthers* parallel and contiguous, 3.5–4 mm long, blue-mauve; pollen pale blue-mauve, fading to yellow. *Ovary* globose, ca. 2 mm long, *style* arched behind the stamens, dividing near the anther apices, 18–20 mm long, *branches* ca. 3 mm long, each shortly to deeply divided (occasionally entire) for up to half their length, ultimately recurving. *Capsule* 4–5 mm long; *seeds* ± globose, 16–21 mm diam., brown. *Chromosome number* $2n = 12$.

Flowering time. (Mid January) February to early April.

FIGURE 5. Morphology of *Lapeirousia rivularis*. Habit and corm × 0.5; flower full size. (Drawn by M. L. Branch.)

Distribution and habitat. *Lapeirousia rivularis* appears to be largely a species of locally wet sites in semiarid southwestern tropical Africa (Fig. 6). The type locality is in western Namibia at the southern end of the Erongo Mountains, and it extends from here to northern Namibia and southern Angola. There are also several records from southern and central Zambia where plants are more robust, perhaps a reflection of the wetter climate. The usual habitat is along temporary streams, seeps, or rock flushes, and in Zambia I have seen it in rocky grassland at poorly drained but not notably wet sites. The species probably also occurs in Zim-

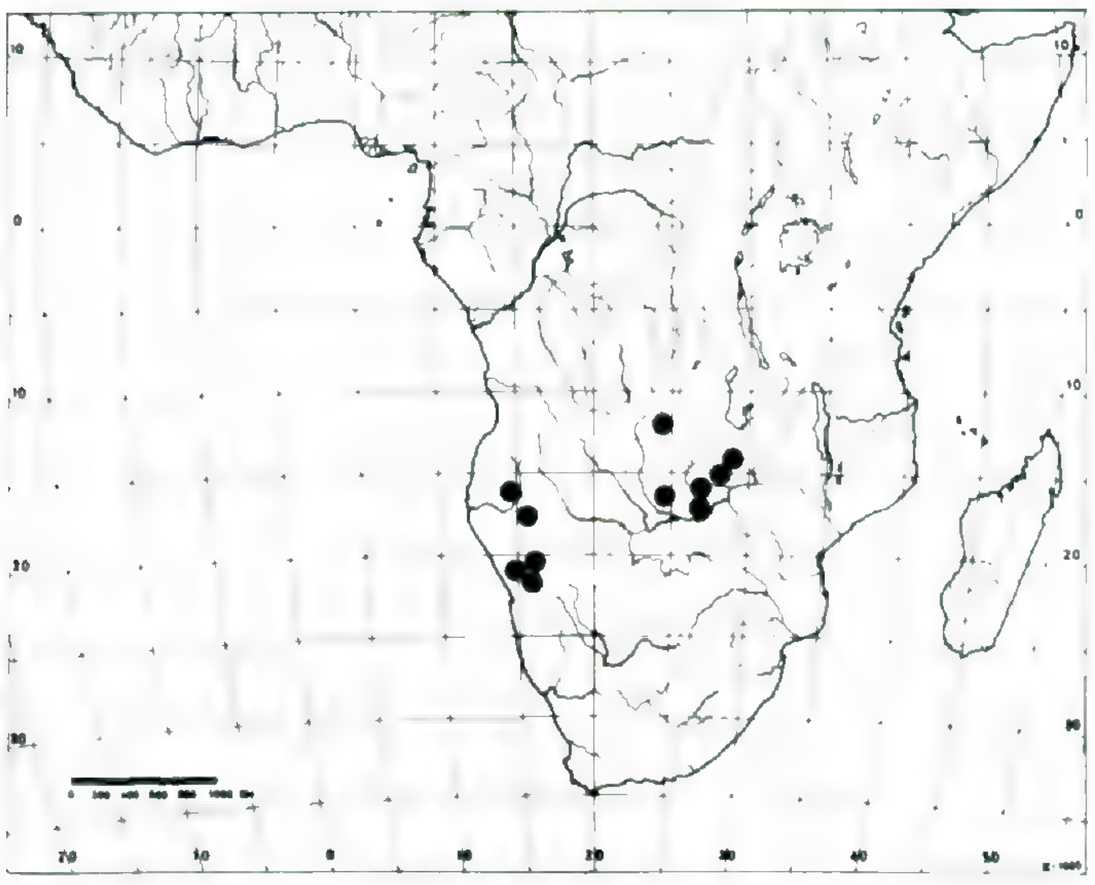

FIGURE 6. Distribution of *Lapeirousia rivularis*.

babwe, but I have seen no specimens that I can confidently refer here although some specimens (e.g., *Eyles 1952*; *Drewe 68*; *Mitchell 1319*) may belong to this species.

Diagnosis and relationships. The zygomorphic, pale blue flower with a perianth tube 7–9 mm long, an upper tepal erect to somewhat hooded over the arcuate stamens and style, and the upper lateral tepals directed forward are the principal features that distinguish *Lapeirousia rivularis* from other tropical African species of *Lapeirousia*. It is probably closely related to the *L. erythrantha* complex and is most often confused with the blue-flowered form of *L. erythrantha*, from which it is difficult to distinguish when dry. The flowers of *L. erythrantha* and *L. rivularis* are similarly colored and proportioned, with a perianth tube 7–9 mm long (–15 mm in *L. erythrantha*) and tepals about as long as the tube. When seen alive, the difference in flower form is striking. *Lapeirousia erythrantha* and its allies have the upper tepal erect to recurved and the upper laterals reflexed. Thus when the flowers are fully open the upper tepals lie in more or less the same horizontal plane as the liplike lower three. Sometimes close examination of herbarium material makes it possible to see this difference, but often the flowers are too distorted. In general *L. rivularis* has a more lax, open panicle typically with 3–5 flowers on the major terminal branches, whereas in *L. erythrantha* the most common type of inflorescence is comparatively dense with flowers crowded terminally on the branches.

It is uncertain whether *Lapeirousia welwitschii*, described by Baker in 1878 and based on specimens collected by Welwitsch in central Angola, is conspecific with *L. rivularis*. The general aspect of the type specimens is similar to dwarfed forms of *L. rivularis*, especially its type, but the flowers are so shrunken and distorted that I hesitate to decide whether *L. welwitshii* is conspecific with *L. rivularis* or is a stunted form of *L. erythrantha*. The name is excluded until plants can be re-collected at the type locality, Pungo Andongo.

The collection from southern Angola, *Baum 958*, is somewhat unusual. Most of the many plants of the collection have unbranched stems, thus the inflorescence is a simple spike, others have one branch, and only a few have more than two branches (one specimen at Z has five branches). That the reduced branching is the result of abnormal growing conditions is as likely as the alternative that the population represents a genetic variant.

History. *Lapeirousia rivularis* was described by the Swedish botanist Hans-Erik Wanntorp in 1971, although he was not the earliest to record the species. It appears to have been first collected in Namibia by the South African zoologist K. H. Barnard, who found it on the northern border of Namibia along the Cunene River in 1921. The type locality of *L. rivularis*, the farm Ameib at the southern end of the Erongo Mountains, is the most southern station for *L. rivularis*, and plants from here can be recognized by the toothlike callus present in the midline of the lower three tepals. This tooth has little taxonomic significance. It appears occasionally in several species of *Lapeirousia*, and I have noted it in a few individuals in populations of the western Cape *L. anceps* and *L. divaricata*, and in some Namibian populations of *L. bainesii* and *L. gracilis*. A tepal tooth is a common feature in *Tritonia* (Ixioideae–Ixieae), in which it defines some sections of the genus (de Vos, 1982), but even in this genus the expression of the character may sometimes vary; a callus or tooth may develop on only one tepal or on none. In *Lapeirousia* the presence of a tooth alone cannot be treated as evidence for recognition of species or even infraspecific taxa.

Additional specimens examined. ANGOLA. CUNENE: between Kiseve and Humbe, 1,100 m, (16°40″ 14°57″) 1 Apr. 1900, *Baum 958* (BM, BR, COI, E, G, K, M, S, Z). NAMIBIA. OVAMBOLAND: 17.15 (Ondangua) Engela Mission, shallow vlei in black sticky clay, 16 Feb. 1959 (BD), *de Winter & Giess 7061* (B, K, M, PRE, SRGH, WIND). OTJIWARONGO: 20.16 (Otjiwarongo) Otjiwarongo, not on summit but high up, 16 Mar. 1980 (BC), *Craven 1129* (WIND). KARIBIB: 21.14 (Uis) Brandberg, Sonuseb, common on top of Sonuseb saddle at water hole, 12 Apr. 1985 (BA), *Craven 2277* (WIND); 21.15 (Karibib) farm Ameib, below Jatow cave, somewhat marshy granite soil, 19 Mar. 1963 (DC), *Giess 13132* (B, M, PRE, WIND); 22 Mar. 1965, *Giess 8452* (K, M, MO, WAG, WIND);

17 Mar. 1963, *Giess et al. 5795* (B, M, PRE, WIND); farm Ameib, coarse sandy, marshy ground below granite outcrops at the Devils Pulpit, 18 Mar. 1968, *Giess 10248* (M, WIND); 5 Apr. 1974, *Merxmüller & Giess 30699* (B, M, K, PRE, SRGH, WAG, WIND); Ameib, Philips Caves, edge of stream, 19 Mar. 1963, *Hardy & de Winter 1420* (B, K, M, PRE, WAG). ZAMBIA. CENTRAL: Lusaka District, campus of the Univ. of Zambia, 19 Jan. 1973, *Strid 2884* (C, K, MO); Lusaka, off Church Road in grounds of Evelyn Hone College, 11 Jan. 1986, *Goldblatt 7537* (E, K, MO, NBG, PRE, S, WAG, WIND); Lusaka, Concord Ranch, 3 mi. S of Chisamba Station, dambo grassland, 19 Jan. 1973, *Benson 214* (K); Mambwa, 27 Dec. 1963, *van Rensburg 2644* (K, SRGH); Kabwe District, Bonanza, 10 km NW of Kabwe, dambo grassland, 19 Jan. 1973, *Kornâs 3023* (K). SOUTHERN: Mazabuka, Ridgeway road, 15 Dec. 1931, *Trapnell 588* (BR, K, PRE, Z); Kafue-Mazabuka, 17 mi. SSE of Nega-Nega, 23 Dec. 1970, *Symoens 13881* (BR, K, M); Siantonola, 10 mi. NNW of Pemba, wet drainage line, 28 Dec. 1962, *Angus 3453* (B, K, WAG). NORTHWESTERN: Kalene Hill, Mwinilunga, seasonally damp ground on sandstone outcrops, 15 Dec. 1963, *Robinson 6051* (M, WAG). WESTERN: Machili, moist pan margins, 24 Dec. 1960, *Fanshawe 6015* (BR, K, LISC, SRGH). WITHOUT PRECISE LOCALITY. NAMIBIA: 1921, *Barnard 201* (SAM); between Kapichu and the Kunene banks, *Barnard 142* (SAM); Mafa, *Barnard 197* (SAM).

4. Lapeirousia erythrantha (Klotzsch ex Klatt) Baker, J. Linn. Soc. Bot. 16: 155. 1878; Handbk. Irideae 168. 1892; Fl. Trop. Africa 7: 351–352. 1898. Geerinck et al., Bull. Soc. Roy. Bot. Belgique 105: 335–344. 1972 (but including *L. teretifolia* and *L. welwitschii*). *Ovieda erythrantha* Klotzsch ex Klatt in Peters, Reise Nach Mossambique, Volume 6 Bot. 2: 516, t. 58. 1864. TYPE: Mozambique: Boror, Caboceira, *Peters s.n.* (holotype, B). Figure 7.

Lapeirousia sandersonii sensu Baker in Fl. Trop. Africa 7: 352. 1898.

Lapeirousia erythrantha var. *briartii* (de Wild. & Durand) Geerinck, Lisowski, Malaisse & Symoens, Bull. Soc. Roy. Bot. Belgique 105: 337–340. 1972. *Geissorhiza briartii* de Wild. & Durand, Compte Rendu Soc. Roy. Bot. Belgique 39: 105. 1900. TYPE: Zaire: Mussimu, Haut Lualaba, *Briart s.n.* (holotype, BR).

Lapeirousia erythrantha var. *rhodesiana* (N. E. Br.) Marais ex Geerinck et al., Bull. Soc. Roy. Bot. Belgique 105: 336. 1972. *Lapeirousia rhodesiana* N. E. Br., Kew Bull. 1906: 169. 1906. Sealy, Bot. Mag. ns. 172: t. 349. 1959. Hepper, Fl. West Trop. Africa, 2nd edition, 3: 141. 1968. TYPE: Zimbabwe (Rhodesia): Mashonaland, headlands between Salisbury and Umtali, *Cecil 154* (holotype, K).

Lapeirousia graminea Vaupel, Bot. Jahrb. Syst. 48: 533. 1912. TYPE: Mozambique: 25 Mile Station (Dondo), in forest, *Schlechter 12238* (holotype, B).

Lapeirousia spicigera Vaupel, Bot. Jahrb. Syst. 48: 547–548. 1912. TYPE: Angola, Huilla: *Antunes 256* (holotype, B).

Lapeirousia plagiostoma Vaupel, Bot. Jahrb. Syst. 48: 547. 1912. TYPE: Mozambique, Station Howesa, rocky slopes, *Tiesler 46* (holotype, B).

Lapeirousia montana Hutchinson, Kew Bull. 1921: 403. 1921, nom. illeg., non *L. montana* Klatt (from S. Africa, Goldblatt, 1972: 52). Hutchinson & Dalziel, Fl. W. Trop. Africa, 1st edition, 2: 376. 1935. *Lapeirousia nigeriensis* R. Foster, Contrib. Gray Herb. 114: 48. 1936, nom. nov. pro *L. montana* Hutchinson. TYPE: Nigeria: top of Zaranda Mountain, 5,800 ft., *Lely 189* (lectotype, K, here designated); Neill's Valley, 2 mi. E of Government Station, Naraguta, *Lely 271* (syntype, K? not seen).

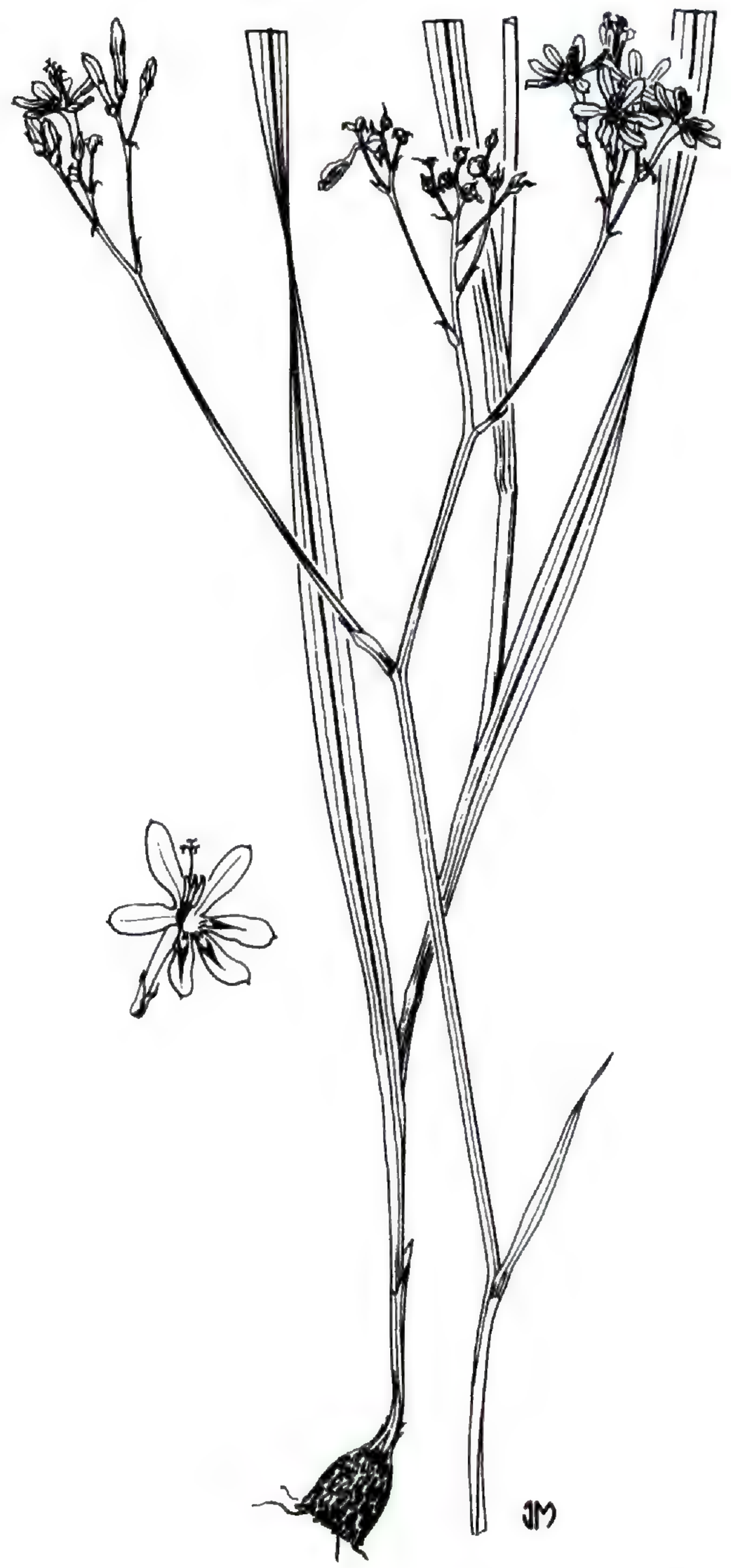

FIGURE 7. Morphology of *Lapeirousia erythrantha*. Habit × 0.5; flower full size. (Drawn by J. C. Manning.)

Plants (15–)20–45 cm high, paniculately branched. *Corm* 8–16 mm wide at the base, tunics blackish, of densely compacted fibers, the outer layers coarsely fibrous, sometimes becoming ± reticulate and fine, then forming a matted layer.

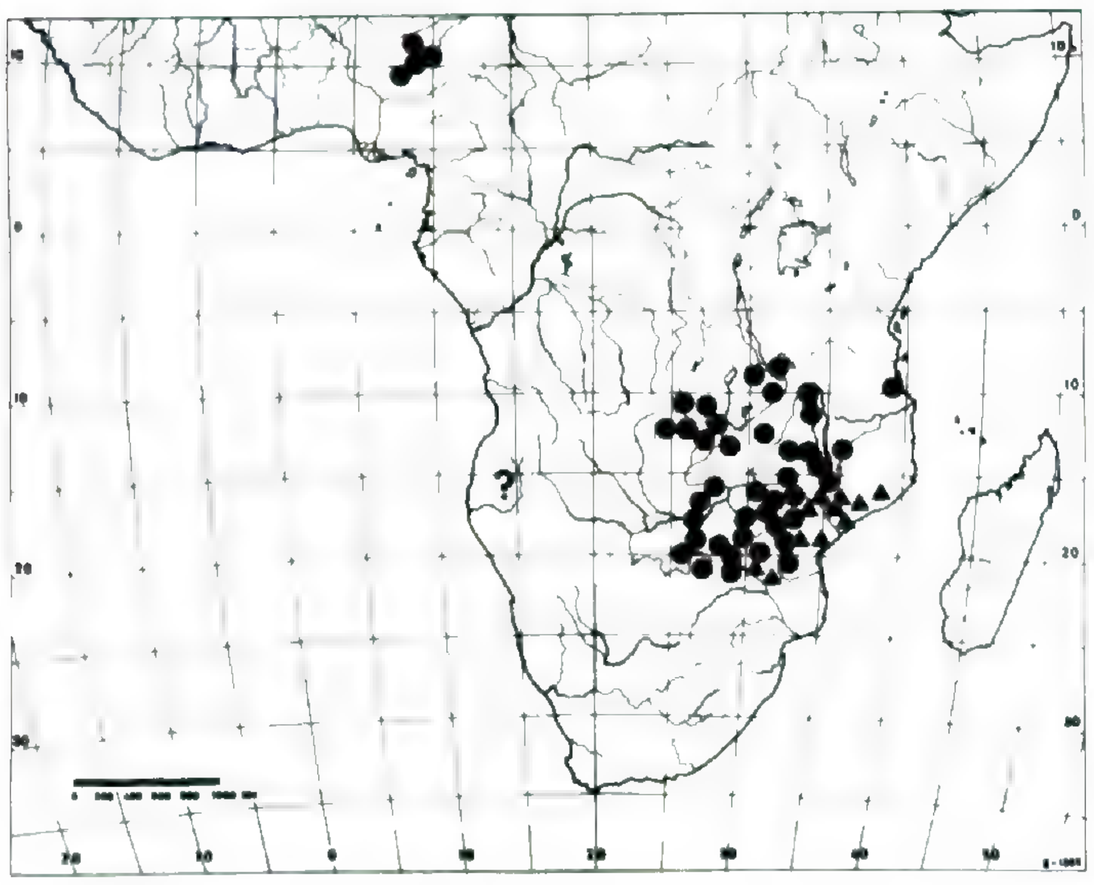

FIGURE 8. Distribution of *Lapeirousia erythrantha*. The question mark indicates the doubtful locality of the type collection of *L. spicigera* from southwestern Angola. Triangles represent red-flowered populations and dots those with blue flowers.

Cataphylls 2, the inner one reaching shortly above ground level, usually dark brown. *Leaves* 3–4, the lower 2–3 longest and ⅓–⅔ as long as the stem, the upper decreasing in size and becoming progressively bractlike above; the basal leaves 2–3, linear to lanceolate, sometimes somewhat falcate, (2–)4–8(–11) mm wide; only the midrib prominent when live. *Stem* compressed and 2-angled below, branched repeatedly, 3-angled above. *Inflorescence* a several- to many-branched panicle, often assuming a corymbose appearance, the ultimate branches bearing (2–)3–6(–8) flowers, these often crowded terminally; *bracts* 3–6 mm long, green below, dry and membranous above in bud, becoming entirely dry and transparent, brownish in the upper third, the outer bract obtuse, usually slightly longer than the inner one, the inner acute or apically bifurcate. *Flower* zygomorphic, either blue-violet having the lower tepals each with a hastate white mark outlined dark blue to purple, or the flower crimson red and then usually without markings but occasionally the lower tepals each with a white median streak (rarely white, either uniformly or with dark markings); *perianth tube* (6–)7–11(–14) mm long, slender below, expanded somewhat and slightly curved near the throat; *tepals* subequal in size, lanceolate-spathulate, acute to obtuse, (6–)7–11 mm long, 2–3(–4) mm wide, lying nearly in one plane, the uppermost tepal held apart from the others and reclined, the lower 3 narrower at base thus ± clawed, set closely together and joined for ca. 1 mm longer than the upper. *Filaments* unilateral and arcuate, 4–6 mm long, inserted ca. 1.5 mm below the mouth of the tube; *anthers* parallel and contiguous, (2.5–)3–4 mm long, pale bluish to white, purple or red; pollen whitish. *Ovary* globose, 1–2 mm long, *style* arched behind the stamens, dividing at mid to upper anther level, ca. 15 mm long, *branches* 1–1.5 mm long, recurving and forked for ⅓–½ their length. *Capsule* 3-lobed, 3–4 mm long, outline of the seeds distorting the walls; *seeds* globose, 2–5 per locule, nearly globose, 1.6–1.9 mm diam., dark brown, weakly to strongly reticulate. *Chromosome number* $2n = 14$ (? = 12 + 2B), 12+0-3B.

Flowering time. (Mid December) late January to March, depending on when the summer rains begin.

Distribution and habitat. As circumscribed here, *Lapeirousia erythrantha* has a wide distribution across south tropical Africa (Fig. 8). It extends from eastern Angola and southern Zaire through Zambia and northeastern Botswana to Zimbabwe, Malawi, western and southern Tanzania, and the coast of central Mozambique. It is a variable species and has differentiated into a number of local races or forms, which are dealt with below. The most common species of *Lapeirousia* in central Africa, *L. erythrantha*, can frequently be found in rocky outcrops throughout its range, or less often in open grassland or woodland. Its frequency in thin soils in rocky sites suggests that the corms are protected in such habitats, while in deeper ground they are accessible to rodents, porcupines, and perhaps other animals. There seems no a priori reason for the apparent preference for rocky habitats, and plants grow well in cultivation in almost any type and depth of soil. The small flowers, conspicuous in the dense inflorescences, are visited and presumably pollinated by large numbers of various bees and wasps that forage for nectar and pollen in warm weather.

Annotations on two specimens indicate that *Lapeirousia erythrantha* is edible (*Simpathu 90*, Victoria Falls; *Buchanan 426*, Shire Highlands, eaten in time of great famine). However, there appears to be no record of the species being significant in the diet of any human population.

Diagnosis and relationships. One of the several species of *Lapeirousia* with a strongly ramified, paniculate inflorescence, *L. erythrantha*, can be distinguished by its relatively small flowers, typically (but not always) soft-textured leaves with a conspicuous midrib, and perianth tube seldom exceeding 12 mm. The flowers are somewhat crowded at the apices of the branches of the inflorescence, and the terminal branches are spikes of 3–8 sessile

flowers. The orientation of the tepals is also distinctive; the tepals lie in more or less the same plane (Fig. 7), with the three lower tepals connate for about 1 mm and held closely together while the upper tepal is recurved and held apart from the others. Similar flowers also characterize *L. sandersonii* and *L. masukuensis*, both of which have a perianth tube 15–25 mm long. *Lapeirousia sandersonii* has different corm tunics and an inflorescence in which the ultimate branches have only one or two flowers.

The Ethiopian *Lapeirousia abyssinica* is closely allied to *L. erythrantha* but has a less ramified inflorescence, and the plants are seldom taller than 15 cm high. The flowers are virtually indistinguishable from those of *L. erythrantha*. The difference in chromosome number, $2n = 12$ in *L. erythrantha* vs. $2n = 8$ in *L. abyssinica*, was a significant reason for my decision to continue to recognize the two species as distinct.

Also closely related is *Lapeirousia setifolia*, a dwarf species of rocky, high-altitude sites in Malawi, Tanzania, and Zimbabwe. Again the flowers of the two species are nearly identical, but the short stature of *L. setifolia* combined with its rather intricately branched inflorescence and chromosome number of $2n = 8$ suggest its separate status.

Lapeirousia rivularis is almost indistinguishable from *L. erythrantha* when pressed, but they have different flowers. In *L. rivularis* the upper tepal is arched forward over the stamens and style branches. This important difference between the two species is generally obscured in herbarium specimens. *Lapeirousia rivularis* grows in seasonally wet sites from central Zambia across southern Angola to northern Namibia, and it thus overlaps in distribution with *L. erythrantha*.

I have raised to species rank *Lapeirousia teretifolia*, a plant of western Zambia and western Shaba, treated by Geerinck et al. (1972) as a variety of *L. erythrantha*. No doubt closely related to *L. erythrantha*, it has particularly small flowers with a pale bluish to white perianth and a highly ramified inflorescence with only one, or rarely two, flowers on the terminal branches. The leaves are terete, a condition that does not occur in any of the several forms of *L. erythrantha*.

Variation. Comprising a number of more or less distinct races or forms, *Lapeirousia erythrantha* presents a difficult problem in circumscribing the species and its close allies. I treat the species fairly broadly and do not attempt to establish an infraspecific taxonomy, such as that of Geerinck et al. (1972) who recognized four varieties in Zaire. The difficulty is the existence of numerous intermediates and parallel forms in different parts of the range. However, it is useful to discuss the main variants here, each of which has been described at some time as a distinct species. The most distinct of the variants is the typical form, which has small to moderate-sized flowers with a deep red perianth (occasional white-flowered plants are albino sports). It occurs in relatively dry sites at low to middle elevations from coastal central Mozambique around Beira inland to southern Malawi and southeastern Zimbabwe. Plants grow in open ground or rocky sites in *Mopane* or dry *Brachystegia* woodland. The unusual intense red perianth (dark maroon on drying) suggests that this form merits taxonomic recognition, but after examining the ample material now at hand, and living populations of red- and blue-flowered forms, I have concluded that they are simply color forms.

Populations of plants with flowers more or less the same size but with purple or blue perianths occur in southern and central Malawi and are identical in all respects but color with plants from populations with either uniformly red or blue flowers. In the Masvingo area of Zimbabwe there are red-flowered populations with large flowers that correspond in size to those of blue-flowered plants that occur in central Zimbabwe and are often referred to *L. rhodesiana*.

In the main part of its range across Zambia and southern Zaire *Lapeirousia erythrantha* is relatively uniform, although flower size seems to decrease moving from east to west and south to north. The small-flowered plants correspond to *L. briartii*, a species described from Zaire. Plants more or less matching this form but with short stature, unusually narrow leaves (generally about 1.5–2 mm wide), and small flowers occur in northwestern Zambia and adjacent western Tanzania. This combination of characters suggests affinity with *L. teretifolia*. However, the 2–4-flowered terminal inflorescence branches of the northeastern Zambian plants and their flat leaf blades are unlike the predominantly 1-flowered inflorescence branches and terete leaves of *L. teretifolia*. I believe that the general similarity here is superficial and does not indicate close relationship. The northeastern Zambian plants presumably represent a regional form of *L. erythrantha*. The name *L. erythrantha* var. *welwitschii* sensu Geerinck et al. (1972) applies to narrow-leafed specimens of *L. erythrantha* otherwise corresponding to the type of *L. briartii*. The type of *L. welwitschii* is from central Angola, and I have not been able to identify it satisfactorily owing to its poor preservation (see excluded species).

A particularly unusual form of *Lapeirousia erythrantha* occurs locally in western Shaba at Etoile (Kalukuluku) Mine (*Symoens 10141*; *Ndjele 1087*; *Lisowski 115, 117*). It has rigid leaves, which appear in the dried material to lack a distinct midrib, and has rather open ramified panicles. The flowers appear to be similar to those in other populations of *L. erythrantha* from Zaire. This may be a race adapted to highly mineralized soils.

In eastern Zimbabwe, populations appear to consist largely of plants with a very open inflorescence and a reduced number of flowers (1–3) on each inflorescence branch. These plants correspond with *L. graminea*, the type of which is from Tete Province, Mozambique.

In western Zimbabwe and adjacent parts of Botswana, plants have rather large flowers with perianth tubes usually 10–14 mm long. These populations are the least well understood of the variants of *Lapeirousia erythrantha* and are sometimes referred to *L. rhodesiana* (or *L. erythrantha* var. *rhodesiana*). The type of *L. rhodesiana* is from Headlands in eastern Zimbabwe and does not correspond exactly to the western Zimbabwe and Botswana plants, which may on further study be found to be a separate species.

A few populations in central and northern Malawi stand out in having flowers with a particularly long perianth tube and have sometimes been referred to *L. sandersonii*. However, their corms and the number of flowers on the inflorescence branches correspond exactly to *L. erythrantha*, as does the chromosome number, $2n = 12$, and karyotype in one population sampled. Moreover, individuals within these populations vary for tube length, which ranges from 12 to 20 mm (e.g., *Goldblatt 7535*).

History. *Lapeirousia erythrantha* was first collected by the German physician and explorer Wilhelm Peters in the years 1842–1848 when he traveled in Mozambique under the patronage of King Friedrich Wilhelm IV. Later the Scottish explorer Sir John Kirk, who accompanied David Livingstone on his Zambezi expedition in 1858, also recorded the species in the lower Shire valley in Mozambique. Kirk collected it again in the following years on subsequent expeditions to the African interior. The species was described by F. W. Klatt (1864), who saw only the Peters collection, and referred to *Ovieda*, a synonym of *Lapeirousia* used from 1815 to 1876.

In the *Flora of Tropical Africa*, Baker (1898) recognized *L. erythrantha* for red-flowered plants, and he referred blue-flowered plants to the Transvaal species, *L. sandersonii*. A collection from Zaire of the common blue-flowered form of *L. erythrantha* was described as *L. briartii* by de Wildeman in 1900. Similar plants from Zimbabwe were assigned to *L. rhodesiana* by N. E. Brown (in 1906), while those from Mozambique were treated by Vaupel (1912) as *L. graminea* and *L. plagiostoma*. A specimen collected in southwestern Angola was referred to *L. spicigera* by Vaupel. *Lapeirousia spicigera* is unusual in having up to 10 flowers crowded on the terminal branches of the few-branched inflorescence. No other specimens of *L. erythrantha* have been recorded from this part of Angola, and there is consequently some doubt about the provenance of the collection.

To this growing number of named blue-flowered forms of *Lapeirousia erythrantha* John Hutchinson in 1921 added *L. montana*, based on specimens from Nigeria. A homonym for a southern African species (Goldblatt, 1972), this name was replaced by *L. nigeriensis* by R. C. Foster (1936). The Nigerian populations were referred to *L. rhodesiana* by Hepper (1968). They correspond most closely to western Zimbabwe plants of *L. erythrantha* in flower size, but the plants are comparatively short in stature.

The treatment of some variants of *Lapeirousia erythrantha* as formal taxonomic varieties by Geerinck et al. (1972) was an attempt to deal with the variation in the species in Zaire. W. Marais (pers. comm.) proposed treating *L. sandersonii* (including *L. masukuensis*) and the southern African and Angolan *L. bainesii* (including *L. otaviensis*) as varieties of *L. erythrantha*, but all four of these are in my opinion separate species, as is *L. teretifolia*, which Geerinck et al. treated as a variety of *L. erythrantha*.

Additional specimens examined (red-flowered and blue-flowered forms, corresponding to the types of *L. erythrantha* and *L. briartii*, respectively, are listed separately).

Red-flowered Forms. MALAWI. SOUTHERN REGION: Blantyre, savanna woodland, Michiru, 4,000 ft., 26 Dec. 1966, *Chimphamba 9* (K, MAL, SRGH); Blantyre, Chichiri campus near upper hostel, 2 Jan. 1966, *Binns 164* (MAL); Blantyre District, 3.6 mi. W of Mpatamanga Gorge, 7 Jan. 1969, *Eccles 223* (K, MAL, SRGH); Lirangwe, ca. 20 mi. N of Blantyre, open ground in woodland, 16 Jan. 1967, *Hilliard & Burtt 4500* (E, K, MAL); Manganja Hills N of the Shire River, 1861, *Waller s.n.* sub *Kirk s.n.* (K); Manganja Hills, Dec. 1861, *Kirk s.n.* (K); Chileka, Blantyre District, 11 Feb. 1947, *Kleinschmidt s.n.* (GH 15726, K); near Chileka Post Office, *Goldblatt 7524* (MAL, MO, NBG, PRE, WAG); foot of Mt. Mulanje, Tinyande Estate at Mulanje Reserve boundary, open woodland, 27 Dec. 1986, *Chapman & Chapman 8315* (MO). MOZAMBIQUE. MOZAMBIQUE: Nampula, 7 Jan. 1937, *Torre 1278* (COI); Nampula, monte Nas-

sapo, andados 23 km de Nampula para Meconandados, 13 Jan. 1964, *Torre & Paiva 9911* (LISC). TETE: Tete, Chioco, at km 48 on the road to Mocubura, 15 Feb. 1968, *Torre & Correia 17670* (LISC). ZAMBEZIA: Serra Tumbine, E of Mlanje town hall, 17 Jan. 1971, *Hilliard & Burtt 6295* (E, LMU); 97 km NE of Mopeia Velha on the road to Quelimane, woodland bordering a vlei, *Pope & Müller 547* (LISC, LMA, MO, SRGH); Namagoa Estate, Mocuba District, Namagoa, 200 ft., Dec.–Jan. 1943, *Faulkner 156* (BR, COI, K, P, PRE, S, SRGH); near Shire River, between the mouth and Morrumbala, Dec. 1858, *Kirk 16* (K). MANICA & SOFALA: Dombe District, above the E bank of the Makuripini 5 km above the confluence of the Haroni, woodland clearing, 6 Jan. 1969, *Bisset 13* (K, LISC, PRE, SRGH); Manica, Moribane (frontier), 17 Nov. 1942, *Salbany 86* (LISC); Chimorio, Garuzo, fazenda Martinoti, 8 Jan. 1948, *Barbosa 814* (LISC); 25 Mile Station (Dondo), 200 ft., 10 Apr. 1898, *Schlechter 12238* (B, K). ZIMBABWE. MASVINGO: Fort Victoria (Masvingo), Jan. 1948, *Fitt s.n.* (SRGH 19039 in BR, K); Mtoko District, Monissi Camp, rocky outcrop, 2,900 ft., 13 Feb. 1962, *Wild 5640* (BR, K, MO, SRGH); 7 mi. E of Fort Victoria, grassy roadside, Dec. 1957, *Miller 4893* (K); 29 mi. ESE of Ngundu Halt on Triangle road, wet vlei at foot of granite hill, 15 Jan. 1963, *Leach 11592* (K, LISC, MO, PRE); Chibi District, kopje near Madzivire Drive, grassland, 30 Dec. 1962, *Moll 484* (K, SRGH); Fort Victoria, Duvali Ranch, 21 Jan. 1948, *Fisher 1387* (PRE), *1390* (SRGH); 5 mi. from Fort Victoria on the Sabie road, wet pan, Jan. 1969, *Goldsmith 10/69* (K, LISC, MO, PRE, SRGH).

Blue-flowered Forms. ANGOLA. MOXICO: W of River Kaperu, grassland, 10 Jan. 1938, *Milne-Redhead 4030* (BR, K, LISC, PRE). HUILA: *Antunes 256* (B) [can this locality be correct?]. BOTSWANA. NORTH EAST: Ramakqwebane area near Tsessebe Station, 6 Jan. 1974, *Ngoni 243* (MO, SRGH); border near Plumtree, sandy flat roadside, 7 Mar. 1961, *Richards 14552* (K, SRGH). CENTRAL: Bakalaka area, between Francistown–Maun road and Marapong, 26 Jan. 1967, *McClintock K73* (K); between Francistown and Nata River, on Maun road, 21 Jan. 1959, *West 3898* (BR, K, LISC, PRE); 22.27 (BB), Selebi, Jan. 1978, *Kerfoot 8007* (PRE). MALAWI. CENTRAL REGION: Lakeview, Dedza Plateau, roadside, 5,500 ft., 22 Dec. 1976, *Pawek 12010* (K, MAL); 15 km N of Ncheu, around granite dome, 9 Sep. 1986, *Goldblatt 7534* (MO); 2 mi. E of the State House, Lilongwe, rock outcrop, 11 Jan. 1984, *May 1* (MAL); Dedza, *Brachystegia* woodland on Kanjoli Hill, 13 Feb. 1967, *Salubeni 563* (K, LISC, PRE, SRGH); Lilongwe, Dzalanyama Forest Reserve, valley NW of Kazuzu hill, 24 Feb. 1982, *Brummitt 16078* (K); road to Dedza Forestry School, around quarry, 9 Jan. 1986, *Goldblatt 7535* (MAL, MO, PRE); Chongoni Forest Reserve, 24 Feb. 1986, *La Croix 2698* (MO). SOUTHERN REGION: Zomba, Old Naisi Road, 11 Jan. 1978, *Masiye 26* (M, MAL, MO, SRGH, Z); Zomba, Old Naisi Road, 1 mi. E of herbarium, rock outcrop, 23 Dec. 1980, *Chapman 5500* (BR, MAL, MO), 5 Jan. 1986, *Goldblatt 7514* (MO); Blantyre District, grassland north of Lundu, 7 Jan. 1986, *Goldblatt 7525* (MO); Zomba, rock outcrop opposite university across Mponda stream, 6 Jan. 1986, *Goldblatt 7521* (MO); Matope, Blantyre, 6 Jan. 1956, *Jackson 1777* (BR, K, MAL); Shire Highlands, Oct. 1879, 1880, *Buchanan 50* (E); 1891, *426* (E) "eaten in time of great famine." NORTHERN REGION: Rumphi District, Luwachi dispensary ridge, 24 Dec. 1972, *Pawek 6122* (MAL); Karonga District, Sangilo Point, 705 m, 2 Jan. 1973, *Pawek 6304* (MAL, SRGH), 24 Feb. 1978, *Pawek 13822* (BR, MO, WAG); Rumphi District, Chiweta, 474 m, near lake shore, 30 Dec. 1986, *La Croix 4255* (MO). MOZAMBIQUE. TETE: Angónia, 2 Dec. 1980, *Macuácua 1363* (MO, PRE, WAG); Chioco, km 49 estrada para Mocubura, 15 Feb. 1968, *Torre & Correia 17677* (LISC); Cabora Bassa, planalto do Songo, 21 Jan. 1973, *Torre et al. 18820* (LISC). NIASA: Mandimba, 9 Dec. 1941, *Hornby 3518* (PRE). NIGERIA. BAUCHI: Vom, Bauchi Plateau, shallow soil on rocks, Dec. 1979, *Young 244* (K); Bauch Plateau, *Lely 259* (K); 3 mi. S of Rishi, Lame District, 3 June 1955, *Sumerhayes 56* (K). PLATEAU: Miago, near Jos, 23 May 1968, *Daramola s.n.* (BR, FHI 61986, K); *Lowe 1330* (K, WAG); Jos, July 1974, *Sharland 429* (K); Jos District, Naraguta, 10 May 1965, *Olorunfemi s.n.* (FHI 55801 in K). TANZANIA. MTWARE: Lindi, Mar. 1952, *Semsei 701* (B, K, PRE); Tendaguru, 100 km NW of Lindi, 17 Feb. 1935, *Schlieben 6010* (B, BR, K, M, P, S, Z). RUKWA: Ufipa, Ilembe, 2,100 m, 18 Mar., *Richards 8781* (K). ZAIRE. SHABA: Elisabethville, 28 Mar. 1912, *Bequaert 294* (BR); mont Namuntamba, forêt claire, 13 Feb. 1987, *Billiet & Jadin 4137* (BR); entre village Kamina et Kyalwe, 3 Jan. 1972, *Bulaimu 311* (BR); Welgelegen, 1912, *Corbisier & Florent 632* (BR); Kafubu, forêt, 21 Mar. 1970, *De Georgi 357* (BR, S); mont Mukuen, 8 Jan. 1957, *Detilleux 361* (BR); Elisabethville, 22 Jan. 1926, *Hirschberg 60* (K, PRE); Feb. 1912, *Homblé 118* (BR); vallée de Kapiri, Feb. 1913, *Homblé 1192* (BR); près de Kipushi, 10 Mar. 1970, *Lissowski 111* (BR); roadside 12 km from Lubumbashi to Likasi, 1,200 m, 18 Feb. 1970, *Lisowski 112* (BR); open forest on hill near Lukuni, 21 km NW of Lubumbashi, 1,300 m, 25 Jan. 1970, *Lisowski 114* (B, K); Lupembe valley, ca. 28°28″ 12°, 27 Jan. 1905, *Kassner 2391* (BR, E, K, P, Z); Chabara, colline cuprifère, 1,430 m, 10 Jan. 1981, *Malaisse 11446* (BR); Mwashya, 935 m, 30 Jan. 1981, *Malaisse 11558* (BR); route Gombela à Poste Luishi, 30 km NE Gombela, 8 Feb. 1982, *Malaisse & Robbrecht 1851* (BR); Fungurume, 15 Feb. 1983, *Malaisse & Robbrecht 2181* (BR); 30 km ESE Kolwezi, colline cuprifère, 1,300 m, 17 Feb. 1982, *Malaisse & Robbrecht 2407* (BR); Haut-Katanga, 12 km S of Elisabethville, 17 Nov. 1928, *Quarré 1017* (BR, K); Haut-Katanga, valley of the Lubumbashi near Elisabethville, Mar. 1933, *Quarré 3103* (BR, K, P, PRE, WAG); Jan. 1938, *5029* (BR, K); Lubumbashi, Feb. 1935, *Quarré 4459b* (BR); vallée de la Kisanga, sol humide, noir, Mar. 1946, *Quarré 8178* (BR); Keyberg, 8 km SW d'Elisabethville, rocky wooded hill, Jan. 1947, *Schmitz 1303* (BR); Jan. 1953, *Schmitz 4303* (BR); rocky hill 10 km S of Elisabethville, Feb. 1954, *Schmitz 4582* (BR, K, NBG); 25 km NW de Elisabethville, forêt claire, 30 Jan. 1959, *Schmitz 6771* (BR); open *Brachystegia* forest, ca. 14 km from Lubumbashi, 17 Feb. 1966, *Symoens 12244* (BR, K); 24 Jan. 1971, *Symoens 14049* (BR, K, M); ancien mine de cuivre de l'Etoile (Kalukuluku), 11 km à Elisabethville, 20 Mar. 1963, *Symoens 10141* (BR, LISC, K, SRGH); 10 Feb. 1966, *Symoens 12206* (B, BR, K); 18 Mar. 1983, *Ndjele 1087* (BR); 21 Feb. 1971, *Lisowski 115* (BR, K); 14 Jan. 1971, *Lisowski 117* (B, BR, K). ZAMBIA. COPPERBELT: Luanshya, grassy dambo, 22 Jan. 1954, *Fanshawe 711* (BR, K, NDO); Luanshya, gravelly pan, 18 Jan. 1955, *Fanshawe 1800* (K, NDO); 23 Mar. 1955 (fr), *Fanshawe 2211* (K, NDO); Solwezi, chipya dambo, 9 Jan. 1969, *Mutimushi 2895* (NDO, SRGH); Solwezi District, N of the Lumwana River, near Lumwana Mission, shallow soil

over rock, 11°49″ 25°7″, 19 Jan. 1975, *Brummitt, Polhill & Chisumpa 13867* (K, NDO, SRGH, WAG); Mufulira, 4,000 ft., rocky shallow soil at riverside, 8 Feb., *Cruse 187* (BR, K); S of Mufulira near Kafue bridge, cliffs and rock outcrops, 17 Jan. 1986, *Goldblatt 7575* (MO); Parklands, Kitwe, bush at the end of Lincoln Ave., 2 Mar. 1961, *Linley 85* (K, LISC, MO, SRGH); Kitwe, hill woodland, 6 Mar. 1964 (fr), *Mutimushi 668* (K, NDO, SRGH); Kitwe, laterite in Miombo, 16 Feb. 1967, *Mutimushi 1810* (BR, K, NDO); Chati Forest Station, rocky hill in Champala Nature Reserve, 14 Jan. 1986, *Goldblatt 7567* (MO, NDO). NORTHERN: Abercorn District, Isanya, 12 Jan. 1952, *Richards 460* (K); flat wet site above escarpment, Chilongowelo, 5 Mar. 1952, *Richards 901* (BR, K); plain of death, Chilongwelo, 4,800 ft., 15 Feb. 1955, *Richards 4495* (BR); Mningi pans, Abercorn, among rocks, 22 Feb. 1959, *Richards 10957* (BR, K, MO); Abercorn (Mbala), Itembwe Gap, 19 Jan., *Richards 18829* (K); Mbala District, St. Paul road, near Kafedro, 5,000 ft., 22 Feb. 1968, *Sanane 52* (K); 4 mi. from St. Paul Mission, Kilala village, among flat rocks and short grass, 7 Mar. 1968, *Sanane 81* (BR, K). NORTHWESTERN: Mwinilunga District, just N of Mwinilunga, shallow soil overlying laterite, 26 Jan. 1938, *Milne-Redhead 4361* (BR, K). CENTRAL: Sanje Hill, *Faden et al., 74/83* (MO, US); Chakwenga headwaters, 100–129 km E of Lusaka, 14 Feb. 1965, *Robinson 6384* (B, M). EASTERN: Fort Jameson (Chipata), Sumbi Hills, 950 m, 3 Jan. 1959, *Robson 1025* (BR, K, LISC, PRE, SRGH); Fort Jameson District, Zingali Hill, 14 Feb. 1961, *Grout 256* (BR, K); Luangwa Valley, siltstone areas near Kapamba River, *Astle 5794* (NDO, SRGH). SOUTHERN: Choma District, Maamba, 40 km N of Choma, 9 Feb., *Chisumpa 454* (K, NDO); Mazabuka District, 158 mi. S of Lusaka, open woodland, 1 Jan. 1958, *Noak 316* (K, SRGH); Mazabuka District, 4 mi. from Chirundi Bridge, mopane woodland, 6 Feb. 1958, *Drummond 5493* (BR, LISC, PRE, SRGH); Batoka Gorge, 3 Feb. 1963, *Mitchell 17151* (B, K, SRGH). ZIMBABWE. MASHONALAND WEST: Lomagundi, Silverside Mine, 20 Jan. 1962, *Jacobsen 1614* (PRE). MASHONALAND EAST: Domboshawa Mission, grassland, 27 Dec. 1971, *Norrgrann 80* (MO, SRGH); Dombashawa, granite slopes, 16 Feb. 1958, *Leach s.n.* (BR, GRA, K, P, SRGH 83649); 3 Apr. 1977, *Grosvenor & Renz 1302* (K, MO, PRE, SRGH); 3 Apr. 1986, *Bayliss 10367* (MO); *Bamps et al. 902* (BR, SRGH); Salisbury District, Ruwa, farm Tanglewood, Dec. 1958, *Miller 5583A* (BR, SRGH). MASHONALAND CENTRAL: Darwin District, Kandeya Native Reserve, 3,200 ft., 17 Jan. 1960, *Phipps 2293* (BR, MO, PRE, SRGH); Sipolilo, below escarpment N of Sipolilo, 30 Jan. 1948, *Whellan 296* (K, SRGH). MANICALAND: Melsetter, Mt. Selinda, farm Gungunyema, Dec. 1939, *Obermeyer 2283* (M, PRE); Inyanga, Nyamaropa Tribal Trust, *Biegel 1741* (MO, SRGH); Makoni, between Umtali and Rusape, near Inyanga road, 29 Feb. 1930, *Friess et al. 4012* (BR, PRE, S); Mtare District, Zimunya's Reserve, sandy open country, 25 Jan. 1959, *Chase 7045* (BR, K, LISC, PRE, SRGH); Kelly's Park, 18 mi. NW of Mtare, 27 Nov. 1948, *Chase 983* (BR, LISC, P, SRGH); Chipinga District, Giriwayo, 1,230 ft., 19 Jan. 1957, *Phipps 34* (K, PRE, SRGH). MASVINGO: Tokwe River, Mashaka–Ft. Victoria road, 15 Mar. 1958, *Leach 8232* (K, SRGH); 5 mi. from Fort Victoria on Sabi road, Jan. 1969, *Goldsmith 11/69* (K, MO, S, SRGH). MATABELELAND NORTH: Nyamandhlovu Pasture Station, Jan. 1953, *Plowes 1540* (K, MO, LISC, SRGH); Shangani, Mar. 1918, *Eyles 953* (K, P, SAM, SRGH); Wankie District, Victoria Falls village, 17 Jan. 1974, *Gonde 47/73* (K, S, SRGH); Victoria Falls, 10 Feb. 1912, *Rogers 13008* (PRE); Wankie National Park, Mopane savanna, 25 Feb. 1967, *Rushworth 229* (BR, K, SRGH); Bulawayo, May 1915, *Rogers 13504* (K, PRE, Z); near Circular Drive, Bulawayo, 31 Jan. 1976, *Cross 352* (K, MO, PRE, SRGH). MATABELELAND SOUTH: Matobo, 6 Dec. 1947, *West 2442* (MO, SRGH); Matopos, Nov. 1922, *Eyles 3752* (SAM); Tuli Experimental Station, Gwanda District, 14 Jan. 1965, *Norris-Rogers 586* (K, SRGH); southern outskirts of Bulawayo, Jan. 1972, *Goldblatt 606* (BOL). MIDLANDS: Gwelo District, Mlezu school, 8 Feb. 1965, *Molife* sub *Biegel 37* (BR, MO, SRGH); Que Que, Feb. 1935, *McLeod 42* (PRE). WITHOUT PRECISE LOCALITY: ZIMBABWE: Matabeleland, Feb. 1886, *Elliot s.n.* (K); South African Goldfields, 1870, *Baines s.n.* (K).

5. Lapeirousia setifolia Harms, Bot. Jahrb. Syst. 30: 278. 1902. *Lapeirousia erythrantha* var. *setifolia* (Harms) Geerinck et al., Bull. Soc. Roy. Bot. Belgique 105: 344. 1972. TYPE: Tanzania. Eastern Livingstone Mountains, Ubena, Tsausingewe District, 2,100 m, Mar. 1899, *Goetze 812* (holotype, B; isotypes, BR, E).

Plants small, 5–10(–15) cm high. *Corm* 10–12 mm diam. at the base, tunics with the inner layers firm and unbroken, becoming decayed and ± fibrous with age, dark brown. *Cataphylls* usually 2, pale and membranous below, brownish apically. *Leaves* 3–7, the lower 2–4 clustered basally, ascending, or the lower leaves spreading, the lowermost longest and exceeding the inflorescence, those above decreasing in size progressively, linear above and 0.5–1 mm wide, usually channeled to above the midline and noticeably broadening toward the base. *Stem* irregularly flexuose and somewhat twisted, several- to many-branched, 3–4-angled. *Inflorescence* a congested pseudopanicle, the ultimate branches bearing 2–4 flowers, the internodes half as long as the bracts; *bracts* herbaceous, often purple-flushed, 4–5 mm long, the inner as long or slightly shorter than the outer, the apices dry and apiculate, recurved. *Flower* zygomorphic, blue to violet, the lower tepals each with a white and dark blue marking in the lower midline; *perianth tube* 8–10 mm long, slender, expanded and curved in the upper 1.5 mm; *tepals* narrowly lanceolate, 7–9 mm long, ca. 2 mm wide, spreading at right angles to the tube. *Filaments* unilateral, exserted 2–2.5 mm from the tube; *anthers* parallel and contiguous, ca. 1.5–2 mm long, yellow (at least when dry). *Ovary* ca. 1 mm long, *style* dividing near mid anther level, the branches ca. 1 mm long, divided for about half their length. *Capsule* globose-trilobed, ca. 2 mm long; *seeds* globose-

oblong, sometimes flattened or lightly angled on the raphal side, 1.3–1.8 × 1–1.3 mm, red-brown. *Chromosome number* $2n = 8$.

Flowering time. February to March.

Distribution and habitat. *Lapeirousia setifolia* has a scattered distribution across south tropical Africa (Fig. 9). Its northern limit is in the highlands of western Tanzania at the northeast end of Lake Malawi, and across the lake on the Nyika Plateau of Malawi. Populations also occur in the Inyanga Highlands of eastern Zimbabwe and in the lower and drier Matopos Hills of southwestern Zimbabwe. The habitat is one typical of *Lapeirousia*, exposed rock outcrops in shallow soil. Dwarf plants from the Chimanimani Highlands of eastern Zimbabwe possibly also belong here, but they have larger flowers and more likely are depauperate *L. erythrantha*.

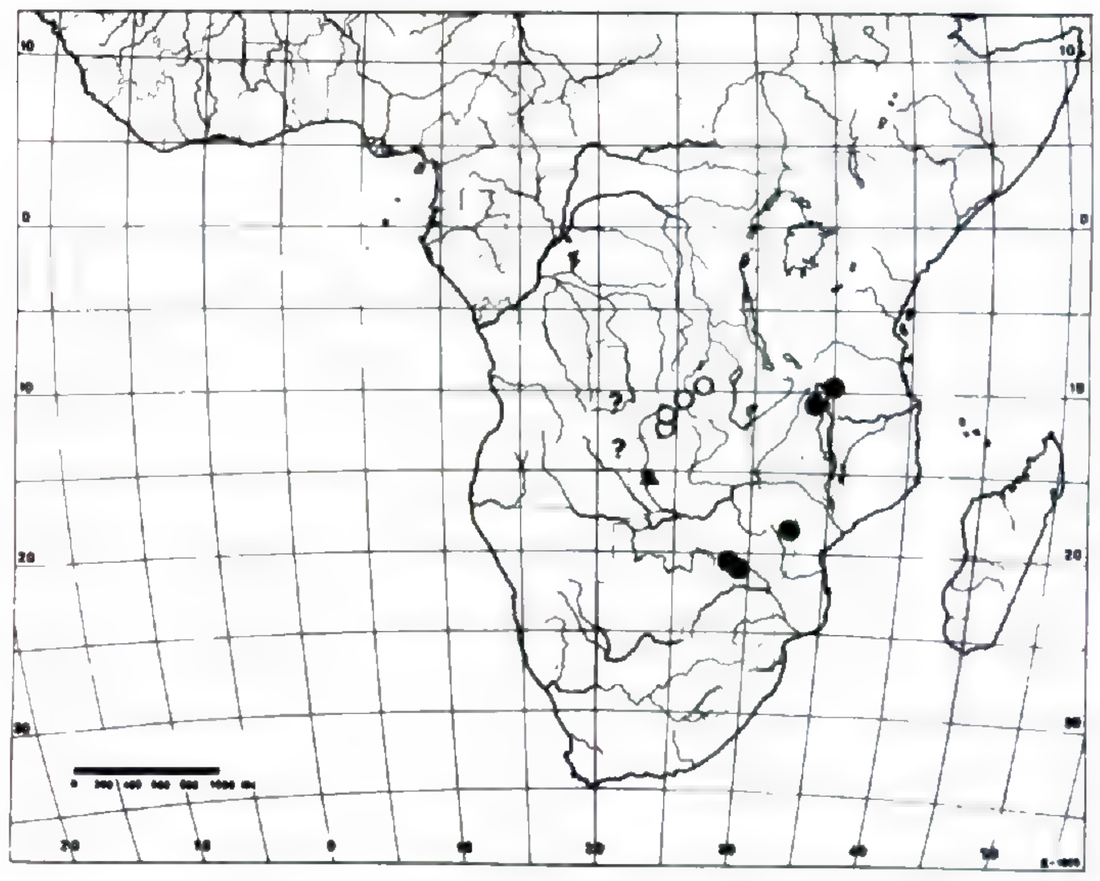

FIGURE 9. Distribution of *Lapeirousia setifolia* (dots), *L. teretifolia* (open circles), and *L. angolensis* (triangle). The question mark indicates uncertainty about the exact placement in Angola of the single collection each of *L. teretifolia* and *L. angolensis*.

Diagnosis and relationships. *Lapeirousia setifolia* can usually be distinguished with ease from *L. erythrantha* and other members of this complex by its low stature, seldom exceeding 15 cm, leaves narrower than 2 mm, and somewhat contorted inflorescence branches. The flowers are fairly typical of the complex, having a violet perianth and relatively short perianth tube, but they are generally smaller than those of most forms of *L. erythrantha*, and they have narrow tepals ca. 2 mm wide and a particularly narrow perianth tube.

Slightly more robust plants from rocky sites in the Matopos area of western Zimbabwe are included here with some hesitation. It is possible that they are dwarfed specimens of the form of *Lapeirousia erythrantha* that occurs widely across south central Africa. However, *L. erythrantha* in western Zambia has large flowers with unusually broad tepals unlike *L. setifolia*. Plants from the higher Chimanimani Mountains of Zimbabwe perhaps belong in *L. setifolia*, but the available specimens are more like *L. erythrantha* although low in stature and with a few straight branches. Their branching pattern and relatively large flowers with broad tepals are quite typical of *L. erythrantha*.

A single gathering from Zaire, *Lisowski 9954b* from the Marungu Plateau, that was assigned to *Lapeirousia setifolia* (as var. *setifolia*) by Geerinck et al. (1972) has larger flowers and bracts than *L. setifolia* and has a poorly ramified inflorescence of weakly twisted branches. It does not seem appropriate to place *Lisowski 9954b* in *L. setifolia*. It is perhaps a stunted form of *L. erythrantha*, which is well represented in Zaire, possibly growing under unusual edaphic conditions, not uncommon in this area of highly mineralized soils.

Additional specimens examined. MALAWI. NORTHERN PROVINCE: Nyika Plateau, shallow soil over rocks, 2,400 m, 14 Mar. 1961, *Robinson 4495* (K, M, MO); Nyika Plateau, Chelinda Bridge, 7,500 ft., 29 Mar. 1970, *Pawek 3421* (B, K, MAL, MO); 12 Apr. 1969 (fr), *Pawek 2160* (K, MAL); 27 Apr. 1973 (fr), *Pawek 6674* (C, MO); Karasamba road 7 mi. E of Chelinda, 4 Mar. 1977, *Pawek 12431* (BR, MO, WAG); Nyika Plateau, 18 Feb., *Richards 14395* (K); Chosi road, Nyika Plateau, 17 Feb. 1976, *Phillips 1227* (K, MAL, MO, WAG); rocks above Chelinda Bridge, 2 Mar. 1967, *Jones & Binns 269* (MAL); Nyika, just after Chosi turnoff, 2,250 m, 14 Feb. 1987, *La Croix 4321* (MO); Nyika Plateau, S of Chelinda camp on the road to Mt. Chosi, among rocks, 10 Mar. 1977, *Grosvenor & Renz 1118* (MO). TANZANIA. IRINGA: Eastern Livingstone Mountains, Ubena, Tsausingewe District, 2,100 m, Mar. 1899, *Goetze 812* (B, BR, E). ZIMBABWE. MASHONALAND EAST: Inyanga, shallow waterlogged soil on granite at Matemma, 11 Jan. 1967, *Plowes 2841* (BR, P). MATABELELAND SOUTH: Matobo District, farm Besna Kobila, shallow soil over rock, Dec. 1954, *Miller 2568* (K, PRE); Mar. 1960, *Miller 7261* (PRE, SRGH); Besna Kobila, grassland, Jan. 1954, *Miller 2063* (K, LISC, SRGH); Matopos, Feb. 1903, *Eyles 1176* (SRGH); Matopos, Amatyundula, 5,000 ft., 22 Dec. 1920, *Borle 43* (PRE, SRGH); Matobo, farm Quasinga, 4,700 ft., Dec. 1953, *Miller 2004* (B, BR, LISC, PRE, S).

6. Lapeirousia teretifolia (Geerinck et al.) Goldblatt, comb. et stat. nov. *Lapeirousia erythrantha* var. *teretifolia* Geerinck, Lisowski, Malaisse & Symoens, Bull. Soc. Roy. Bot. Belgique 105: 342. 1972. TYPE: Zaire. Shaba: Plateau de la Manika, env. 2 km W de Katema, 20 Jan. 1969, *Lisowski, Malaisse & Symoens 182* (lectotype, BR, here designated—no holotype was indicated from among

the several duplicates of the type collection; isotypes, K (also EBV, POZ not seen)).

Plants 20–40 cm high. *Corm* 9–13 mm diam., tunics dark brown to blackish, woody, the outer layers breaking into vertical parallel segments. *Cataphylls* 1 or 2, the upper (or only) one reaching shortly above the ground, dark brown, apparently dry by anthesis. *Leaves* 3–4, the lowermost inserted near the ground and longest, the upper leaves decreasing in size above, the longest about half as long to as long as the stem, ± terete to elliptic in section, without a discrete midrib, rigid, 1–1.5 mm diam. *Stem* ± terete below, lightly 3–4-angled above. *Inflorescence* a rounded to columnar panicle, the main axis usually dominant, the terminal branches 1–2(–3)-flowered; *bracts* (2.5–) 3–4 mm long, ± membranous, transparent below, rust-brown above or brownish entirely, the inner bract slightly longer than the outer. *Flowers* weakly zygomorphic, whitish to pale lilac, the lower tepals each with a darker blue to violet median streak in the lower midline; *perianth tube* 4–5 mm long, slender, slightly expanded above; *tepals* subequal, spreading ± at right angles to the tube, 5–6 mm long, the uppermost held apart from the others, the lower 3 held closely together. *Filaments* unilateral, erect, 3.5–4 mm long, exserted 2–2.5 mm from the tube; *anthers* parallel and contiguous, 2–3 mm long; pollen yellow. *Ovary* globose, 1–1.5 mm long, *style* arching behind the stamens, dividing at mid anther level, branches ca. 1 mm long, usually divided for about half their length, sometimes for less. *Capsule* and *seeds* unknown. *Chromosome number* unknown.

Flowering time. February to April.

Distribution and habitat. *Lapeirousia teretifolia* is a fairly local endemic of interior central Africa. It occurs in southern Zaire on the Manika Plateau where it extends from the Parc National de l'Upemba in the north to Musokantanda in the southwest; in Zambia it is restricted to the Mwinilunga District in the northwest; and there is one record from Cacumbe, a locality I have not been able to place, in northeastern Angola. Collection information indicates that *L. teretifolia* grows in seasonally moist or waterlogged ground.

Diagnosis and relationships. *Lapeirousia teretifolia* is a member of the tropical African *L. erythrantha* complex, with which its general form and flower correspond, yet it merits species recognition. It has a more or less terete leaf, an open paniculate inflorescence with the main terminal branches 1–2- or rarely 3-flowered, a low stature, and somewhat smaller flowers than are normally found in *L. erythrantha*. Flower color also differs; the perianth is whitish to pale blue or lilac, whereas *L. erythrantha* has blue or red flowers. *Lapeirousia teretifolia* occurs partly within the range of *L. erythrantha* and, as indicated by collection data, in rather wetter habitats.

History. First collected in 1938 by E. W. Milne-Redhead, *Lapeirousia teretifolia* has remained difficult to place. It was treated as var. *teretifolia* of the widespread *L. erythrantha* by Geerinck et al. (1972), but it seems altogether more distinctive than the several forms of this widespread species and has accordingly been raised to full species rank.

Additional specimens examined. ANGOLA. LUNDA: Cacumbe, near River Cacumbe, 6 Dec. 1946, *Gossweiler 13942* (K). ZAIRE. SHABA: env. de Katema, 12 Jan. 1971, *Lisowski et al. 13243* (BR); plateau de Manika, près de Katema, 12 Jan. 1971, *Lisowski et al. 13302* (B, BR, K); 35 km SW Kolwezi vers Musokatanda, plateau de Manika, 17 Feb. 1982, *Malaisse & Robbrecht 2349* (BR, K); Parc National de l'Upemba, 13 Feb. 1948, *de Witte 3341* (BR, K, WAG). ZAMBIA. NORTHWESTERN: Mwinilunga District, Kalenda plain below the W side of Matonchi Hill, 1,300 m, 18 Feb., *Hooper & Townsend 162* (K, SRGH); Kalenda plain opposite Matonchi farm, seasonally inundated shallow soil over laterite, 18 Nov. 1937, *Milne-Redhead 3301* (BR, K, PRE); Kalenda Ridge W of Matonchi farm, laterite, among *Vellozia*, 22 Jan. 1938, *Milne-Redhead 4280* (BR, K, LISC, PRE); Mwinilunga District, Luakera Falls, sandy slope, 25 Jan. 1938, *Milne-Redhead 4339* (BR, K, LISC, PRE); Matonchi farm, peaty soil, 19 Nov. 1962, *Richards 17294* (K); 15 km W of Kalene Hill, 14 Jan. 1963, *Robinson 6031* (BR, K, M, SRGH); Ikelenge, Mwinilunga District, 16 Apr. 1963, *Robinson 6597* (K, SRGH), 2.1960, *Pinhey 7* (SRGH).

7. **Lapeirousia angolensis** Goldblatt, sp. nov. TYPE: Angola. Moxico: a few mi. W of River Kaperu (Kapelu), boggy grassland, 10 Jan. 1938, *Milne-Redhead 4037* (holotype, K; isotypes, BM, BR, LISC, P, PRE).

Plantae 24–30 cm altae, tunicis cormi atrobrunneis, foliis teretibus vel ellipticis, inflorescentis paniculatis paucifloris, ramis terminalibus 1–2 florum, bracteis (4–)5–6 mm longis, floribus pallide violaceis, tubo perianthii 3.3 mm longis, tepalis 13–14 mm longis, filamentis ca. 6 mm longis, exsertis 5 mm tubo.

Plants 24–30 cm high. *Corm* 13–16 mm diam., tunics dark brown to blackish, composed of hard layers of densely compacted fibers, the outer layers breaking into parallel vertical sections. *Cataphylls* 2, membranous and dark brown, the inner one reaching shortly above the ground. *Leaves* 2–3, the lowermost inserted near the ground and longest, about half as long to as long as the inflorescence,

the upper leaves decreasing in size progressively, ± terete to elliptic in section, without a discrete midrib, rigid, 1–1.5 mm diam. in the middle. *Stem* weakly compressed, 2-angled below, 3-angled above the branches; branching divaricate. *Inflorescence* a rounded panicle with relatively few flowers, the main axis usually dominant, the terminal branches 1–2-flowered; *bracts* (4–)5–6 mm long, ± membranous, green below, rust-brown above, becoming brownish entirely, the inner slightly longer than the outer. *Flowers* zygomorphic, pale violet, the lower tepals each with a pale yellow median streak edged in purple on the lower midline; *perianth tube* 3.3 mm long, slender, slightly expanded above; *tepals* subequal (their orientation uncertain), ± differentiated into a claw below, 12–14 mm long, the limb lanceolate, 1.5–2 mm wide, the margins undulate, the upper tepal apparently held apart from the others, the lower 3 tepals united below for ca. 2 mm and held closely together. *Filaments* unilateral, erect, ca. 6 mm long, exserted 5 mm from the tube, reddish; *anthers* parallel and contiguous, 3.5 mm long, violet; pollen pale. *Ovary* globose, ca. 1.5 mm long, *style* arching behind the stamens, dividing toward the apex of the anthers, branches ca. 1.4 mm long, undivided, recurving. *Capsule* and *seeds* unknown. *Chromosome number* unknown.

Flowering time. February to April.

Distribution and habitat. *Lapeirousia angolensis* is known only from three gatherings made in western Zambia and eastern Angola (Fig. 9). It occurs in boggy grassland, probably in seasonally inundated areas. This type of habitat is most often associated with *L. rivularis* and may indicate a phylogenetic relationship between the two.

Diagnosis and relationships. The most unusual feature of *Lapeirousia angolensis* is its flower with long narrow tepals that greatly exceed the fairly short perianth tube. The tepals appear to be subequal, but the lower three are connate for ca. 2 mm more than the upper three, and hence are shorter. I have not seen live material, and the flower description is a reconstruction that may not be entirely accurate. Clearly the flower is substantially different from that of any other species of the *L. erythrantha* complex. The tube is only 3.3 mm long and does not or barely exceeds the bracts, and the unusually long tepals are thus at least three times as long. The union of the lower three tepals for ca. 2 mm is an additional feature that separates *L. angolensis* from the other species in the complex. The narrow terete leaf is reminiscent of *L. teretifolia*, but the lax panicle and larger bracts and flowers are quite different from this small-flowered species. The style branches are undivided, a feature that is not uncommon in the tropical African species of *Lapeirousia*, and this helps little in placing the species.

History. *Lapeirousia angolensis* is poorly known, having been collected just three times, first by a Mlle. Kiener prior to 1896, at Haut-Zambèse, a locality too vague to be placed. Later collections are from eastern Angola and western Zambia, in areas that are seasonally inundated. Until now the species has not been associated with any other, although it bears a fair resemblance to *L. erythrantha*.

Specimens examined. ANGOLA. MOXICO: a few mi. W of River Kaperu (Kapelu), boggy grassland, 10 Jan. 1938, *Milne-Redhead 4037* (BM, BR, K, LISC, PRE). ZAMBIA. WESTERN: Mongu flood plain, damp grassland, 29 Jan. 1966, *Robinson 6830* (K). WITHOUT PRECISE LOCALITY: ?ZAMBIA: Haut-Zambèse, *Kiener s.n.* before 1896 (P).

8. Lapeirousia abyssinica (R. Br. ex A. Richard) Baker, J. Linn. Soc. Bot. 16: 155. 1878; Fl. Trop. Africa 7: 351. 1898. Andrews, Flow. Pl. Sudan 3: 293. 1956. Cufodontis, Enum. Pl. Aethiopiae Sperm. 2: 1592. 1972. *Geissorhiza abyssinica* R. Br. ex A. Richard, Tent. Fl. Abyssinica 2: 308. 1850. TYPE: Ethiopia: Maigoigoi ad Dobre Sina, *Quartin Dillon & Petit s.n.* (lectotype, P, here designated; isolectotype, BR); Selleuda prope Adoua, *Quartin Dillon s.n.* (syntype, P); Maigoigoi, *Schimper s.n.* (syntype, P). [*Geissorhiza abyssinica* R. Br. in Salt, Voyage to Abyssinia, Appendix 1. 1814, nom. nud.] Figure 10.

Montbretia abyssinica Hochst. ex A. Richard, Tent. Fl. Abyssinica 2: 308. 1850. TYPE: Ethiopia: collibus prope Adoua, flor. et fruct. Octobre, *Schimper 329* (lectotype, P, here designated; isolectotypes, BM, BR, G, K, M, P).

Montbretia gallabatensis Schweinf. ms (*Schweinfurth 1*, BM, G, K, P).

Plants generally small, 9–15 cm high but occasionally to 35 cm, sparsely branched. *Corm* 8–12 mm diam., tunics brown to gray, densely fibrous, the outer layers becoming finely fibrous and reticulate. *Cataphylls* 2, the inner one pale and membranous, reaching shortly above the ground, the outer shorter and dark brown. *Leaves* 3, the lower 2 at least usually inserted near ground level, the lowermost longest and about as long as to slightly exceeding the inflorescence, lanceolate, 3–5 mm wide in the midline. *Stem* compressed and

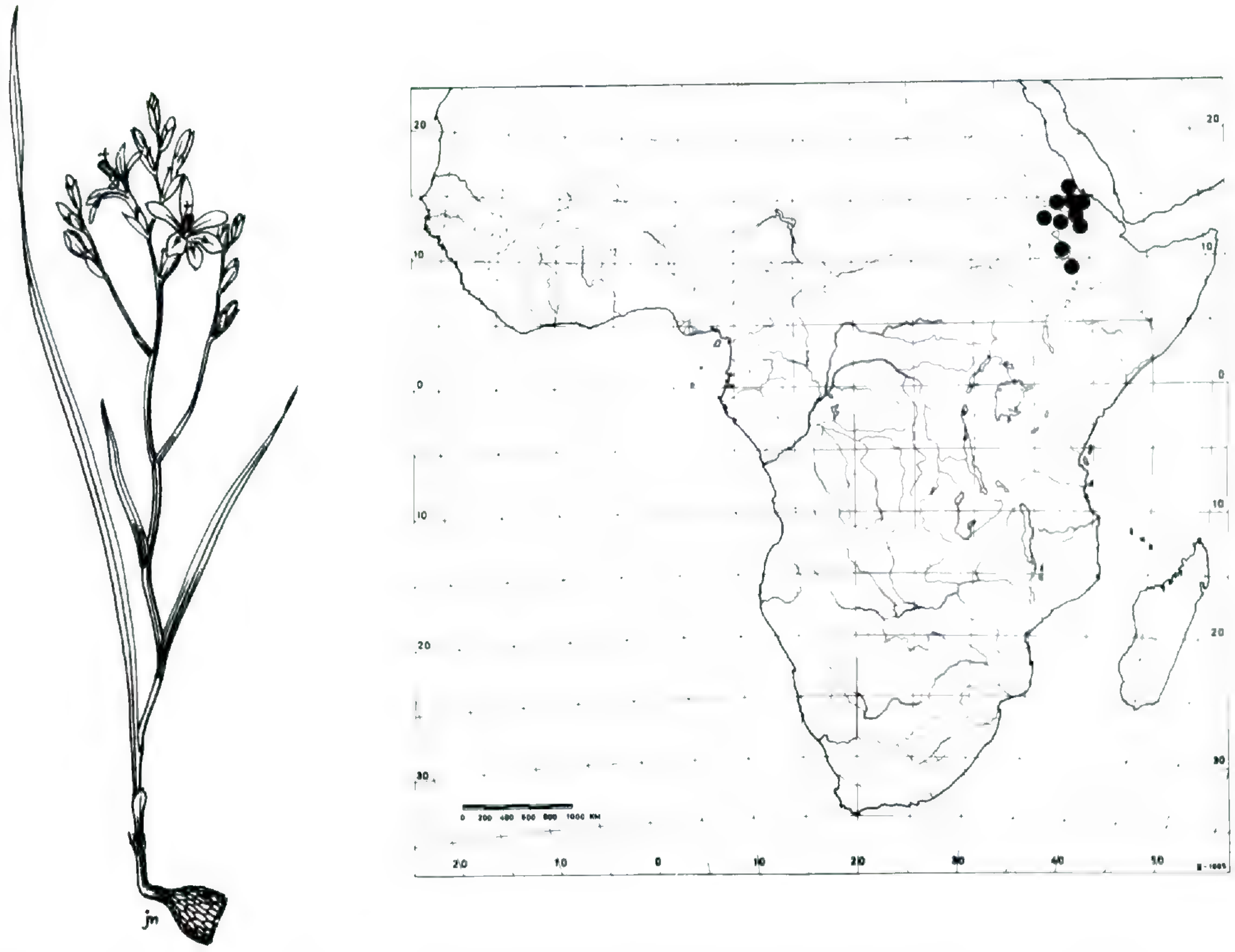

FIGURE 10. Morphology and distribution of *Lapeirousia abyssinica*. Habit × 0.5. (Drawn by J. C. Manning.)

2–3-angled, sometimes narrowly winged above. *Inflorescence* a spike or few-branched pseudopanicle, the main axis 5–7-flowered, the secondary axes with fewer flowers; *bracts* herbaceous, often flushed red to purple, becoming dry in late flower, 6–8 (–10) mm long, the outer bract nearly always exceeding the inner. *Flower* zygomorphic, violet, the lower 3 tepals each with a white median streak edged with a darker band of purple in the lower midline; *perianth tube* ± straight, narrowly funnel-shaped, ca. 9 mm long; *tepals* unequal, lanceolate, the lower 3 horizontal to descending, held close together and forming a lip, ca. 9 mm long, to 2 mm wide, the upper 3 larger, the uppermost ± erect, the upper laterals reflexed, ca. 9 mm long, to 3 mm wide. *Filaments* ca. 6 mm long, unilateral, exserted 3 mm from the tube; *anthers* parallel and contiguous, ca. 3 mm long, pale gray; pollen whitish. *Ovary* ovate-obovate, ca. 2 mm long; *style* unilateral, arching behind the stamens, dividing between the middle and apex of the anthers, branches ca. 2 mm long, barely notched apically. *Capsules* globose-trigonous, 3–4 mm long, showing the outline of the seeds; *seeds* red-brown, globose, ca. 1.2 mm diam. *Chromosome number* $2n = 8$.

Flowering time. Late August to early October.

Distribution and habitat. *Lapeirousia abyssinica* is fairly widespread in the northern half of Ethiopia, where it occurs in shallow soils, usually in rocky sites from northern Shoa Province in the south to Eritrea in the vicinity of Keren in the north. The record indicates that the species is most common in Tigray, the origin of numerous collections. It is recorded from a variety of substrates but is apparently most often found associated with limestone rocks. A collection from "Gallabat near Matamma" (*Schweinfurth 1*) is probably from eastern Sudan close to the Ethiopian border, and is so cited by Andrews (1956).

Diagnosis and relationships. Evidently closely related to *Lapeirousia erythrantha*, and clearly a member of this tropical African species complex, *L. abyssinica* is a plant of low stature with a relatively few-branched to unbranched inflorescence that is essentially a spike. The main axis has 5–7 flowers and the branches typically fewer. The flowers are virtually identical to those of *L. erythrantha* in their blue-violet color, white and dark blue nectar guides on the lower tepals, and erect to reflexed upper tepal. The chromosome number is $2n = 8$ in the one population counted

(Goldblatt, 1990b), whereas *L. erythrantha* has a basic diploid number of $2n = 12$.

History. First collected by Henry Salt in Tigray, northern Ethiopia in 1810–1811, *Lapeirousia abyssinica* was listed without description by Robert Brown as *Geissorhiza abyssinica* in the *Appendix to Salt's Travels* (Salt, 1814). Schimper used the name for some of his collections of the species, and Achille Richard validated it in 1850. In the same work Richard described *Montbretia abyssinica*, validating Hochstetter's manuscript name that appeared on the labels for *Schimper 329*. Although undoubtedly conspecific, *Geissorhiza abyssinica* and *Montbretia abyssinica* are based on different type specimens. *Geissorhiza abyssinica* was transferred to *Lapeirousia* by J. G. Baker in 1876.

Additional specimens examined. ETHIOPIA. ERITREA: near Asmara, 7,600 ft., thin soil, flat open land, 29 Aug. 1954, *Colville 19* (K); Keren road 20 mi. NW of Asmara, sandy waste ground around granite boulders, 26 Aug. 1959, *Mooney 8071* (BR, K, S); Mt. Presso, Scimenzana, 2,500 m, 28 Aug. 1902, *Pappi 814* (BR, G, GH, MO, P, U); Scimenzana, Monti Presso, Senafé, 2,500 m, 28 Aug. 1902, *Pappi 816* (P, S). GOJAM: near Ejube, 15 mi. S of Debra Marcos, 10°15″ 37°48″, 7,000 ft., 11 Sep. 1957, *Hallier 931* (K). GONDER: Gondar, *Rochet de Hericourt s.n.* (P). SHOA: Royaume de Choa, 1847, *Rochet de Hericourt s.n.* (P); Muger valley, ca. 100 km N of Addis Abeba, gypsum hill, 1,800 m, 9°30″ 38°25″, *Edwards et al. 97* (MO). TIGRAY: 40 km S of Kwiha, 2,100 m, gentle slopes on limestone, 13°11″ 39°32″, 12 Aug. 1973, *Gilbert & Getachaw 2625* (K); 3 km N of Adua bridge, Mai-Gougae road to Axum, 1,820 m, slate, 14°9″ 38°38″, 22 Aug. 1973, *Aweke & Gilbert 747* (K, WAG); 37 km S of Quiha, road to Maichew, 2,150 m, 5 Sep. 1970, *de Wilde 6984* (BR, M, MO, WAG); 8 km SW of Inda Selassie on Gondar road, 1,830 m, shallow soil over basalt, seasonally waterlogged, 29 Aug. 1973, *Gilbert & Getachaw 2919* (C, K); near the pass of Atbara, sand, *Salt 37* (BM); valee d'Adoua, Aug. 1839, *Quartin Dillon & Petit s.n.* (P); prope Adouam, Oct. 1839, *Schimper 645* (BM, G, P); Shire, 1853, *Schimper s.n.* (P); 37 km S of Quiha, road to Maichew, dry limestone hills, low shrubland, 5 Sep. 1970, *Amshoff 6984* (MO). SUDAN: Gallabat, near Matamma, 24 June 1861, '*Montbretia gallabatensis* Schweinf.', *Schweinfurth 1* (BM, G, K, P) (possibly in Ethiopia). WITHOUT PRECISE LOCALITY: ETHIOPIA: Abyssinia, *Pearce s.n.* in 1820 (BM); 1861, *Parkyn s.n.* (K); vallée Mareb, *Rochet de Hericourt s.n.* (BM); Aaosa, 6,000 ft., 8 Sep. 1852 (fr), *Schimper 563* (P (2)); Woina, 6,000–7,000 ft., 24 Aug. 1852, *Schimper 563* (BR, K, P).

9. Lapeirousia masukuensis Vaupel & Schlechter, Bot. Jahrb. Syst. 48: 545–546. 1912. TYPE: Mozambique. Inhambane: Masuku forest, 10 Feb. 1898, *Schlechter 12109* (holotype, B; isotypes, BR, COI, G, K, P, PRE, SAM).

Plants 40–60 cm high. *Corm* campanulate, ca. 15 mm diam. at the base, light brown, tunics coriaceous with a reticulate surface, the outer layers decaying to become coarsely fibrous. *Cataphylls* usually 2, membranous, light brown, the upper one longer and reaching shortly above ground level. *Leaves* 4–6, the lowermost inserted close to the ground and largest, the remaining becoming progressively smaller above, the longest usually slightly exceeding the inflorescence, narrowly linear-lanceolate, the midribs prominent, 3–6 mm wide near the midline. *Stem* compressed and 2-angled to winged below, 3-angled and lightly winged above the branches. *Inflorescence* a branched spike or pseudopanicle, the main axis ± straight and dominant, the major ultimate branches forming spikes of 5–9 flowers, the flowers often crowded with the bracts overlapping and (1–)1.5–2 internodes long; *bracts* herbaceous at anthesis, becoming dry and scarious toward the end of flowering, then either pale throughout or brownish above and pale below with streaks of brown on the nerves, 5–7 mm long, the inner bract about as long as the outer or slightly shorter. *Flowers* zygomorphic, either blue to violet or greenish cream, the lower tepals each with a purple to red and white hastate median streak in the lower half; *perianth tube* cylindric, (15–)20–25 mm long, slightly expanded in the upper 4 mm; *tepals* subequal, 8–10 mm long, lanceolate, ca. 3 mm wide, spreading at right angles to the tube and lying in ± the same plane, the upper tepal held apart from the others. *Filaments* unilateral, ± erect, ca. 5 mm long, exserted 2.5–3 mm from the tube; *anthers* parallel and contiguous, 3.5 mm long, probably pale yellow when live. *Ovary* ca. 1.5 mm long, style unilateral and arching behind the stamens, dividing near the upper ⅓ of the anthers, the branches ca. 2 mm long, divided for about ½ their length. *Capsules* depressed-globose, ± 3-lobed and showing the outline of the seeds, ca. 5 mm diam.; *seeds* globose, ca. 2 mm diam. *Chromosome number* unknown.

Flowering time. February to April.

Distribution and habitat. *Lapeirousia masukuensis* is restricted to southeastern tropical Africa, where it extends from coastal central and southern Mozambique in the provinces of Inhambane and Maputo (Sul do Save) westward into the lowlands of the eastern Transvaal of South Africa and southeastern Zimbabwe (Fig. 11). There is an apparent gap in the distribution between the Kruger National Park on the Transvaal border and the Mozambique coast, but this may be due to inadequate sampling in interior Mozambique. A single

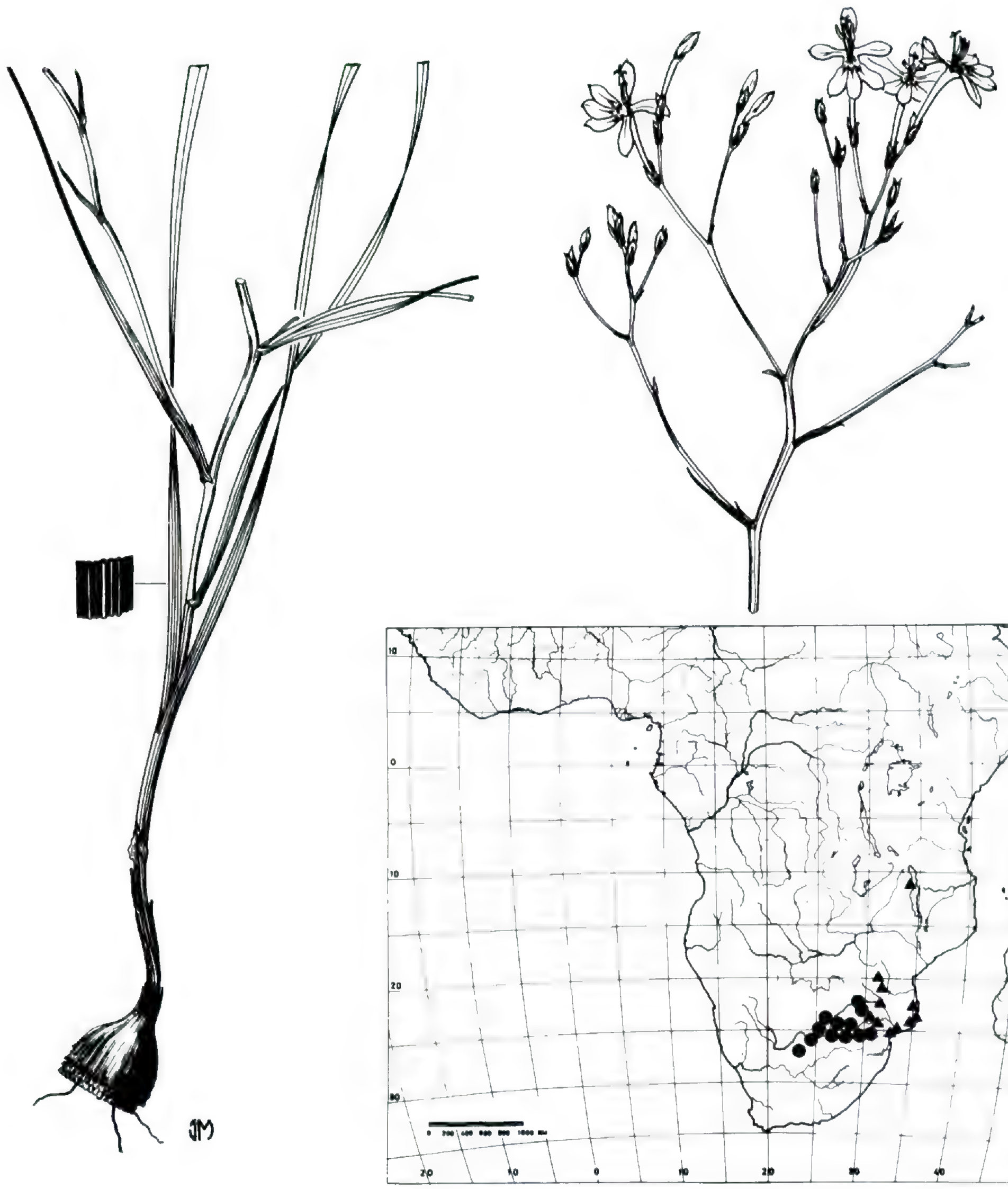

FIGURE 11. Morphology and distribution of *Lapeirousia sandersonii* (dots) and distribution of *L. masukuensis* (triangles). Habit and inflorescence × 0.5; leaf detail × 1.5. (Drawn by J. C. Manning.)

collection from northern Malawi is provisionally referred to this species although its identity remains uncertain. The collection data make it clear that *L. masukuensis* prefers relatively wet habitats. Most specimens are recorded as growing in vleis, the edge of swamps, or in seasonally waterlogged flats.

Diagnosis and relationships. The comparatively tall stature, usually over 45 cm high, alternate branching pattern, ultimate inflorescence branches bearing 5–9 apically crowded flowers, and the long straight perianth tube 20–25 mm long are the main distinguishing features of *Lapeirousia masukuensis*. Plants from the Mozambique coast are described as having greenish flowers with red markings, an unusual color in the genus. However, in the eastern Transvaal, Zimbabwe, and Malawi *L. masukuensis* has flowers with a dark blue-violet perianth with white markings that are typical of related species, such as *L. erythrantha* and *L. sandersonii*. The long perianth tube and general appearance of the flowers, including their color, suggest a relationship with the western Transvaal and Botswana species *L. sandersonii*, and it is usually under this name that specimens of *L. masukuensis* have been placed in herbaria until now. *Lapeirousia sandersonii* is a shorter plant, rarely exceeding 35 cm, with a dichotomous and often intricately branched habit, and the ultimate branches of the inflorescence have one, two,

or rarely three flowers. The corms of the two species also differ, those of *L. masukuensis* being relatively small and having the outer tunic layers fibrous and reticulate, whereas the larger corms of *L. sandersonii* have dark brown tunics that decay irregularly into smooth vertical strips. The corms of *L. masukuensis* resemble closely those of *L. erythrantha* with which it is perhaps most closely allied.

Plants from the Transvaal and Zimbabwe are more variable than those from Mozambique and particularly so in regard to the length of the perianth tube and the number of flowers on the terminal branches of the inflorescence. Generally plants from the Transvaal and Zimbabwe have five or six flowers per branch compared with 6–9 in Mozambique, and the perianth tube is 15–22 mm long. A notable example is *Mauve 4326*, 10 m N of Abel Erasmus Pass, which has some flowers with a perianth tube just 15 mm long, while others have a tube up to 22 mm. It is difficult to explain such gross variation in a feature such as perianth tube length, but this degree of variability is noted in a few collections of other tropical African *Lapeirousia*, e.g., *L. bainesii*, *L. sandersonii*, and *L. erythrantha*.

History. Discovered in 1898 by the widely traveled German botanist and prolific collector Rudolf Schlechter, *Lapeirousia masukuensis* was described by Vaupel and Schlechter in 1912. It appears to be comparatively rare, particularly in Zimbabwe and Mozambique. An early collection made by the French missionary Henri Junod at Shilouvane in the Transvaal bears the manuscript name *L. junodii* N. E. Br., indicating that Brown also considered the species distinct from *L. sandersonii*.

Additional specimens examined. MALAWI. NORTHERN PROVINCE: 20 mi. NW of Rumphi, 1,400 m, 11 Mar. 1978, hard, packed, rocky soil, *Pawek 14048* (K, MAL). MOZAMBIQUE. INHAMBANE: Quissico, 28 Feb. 1955, *Exell, Mendonca & Wild 703* (LISC, SRGH); between Morrumbene and Massinga, 26 Feb. 1955, *Exell, Mendonca & Wild 652* (LISC, SRGH); Inhambane-Velho, June 1938, *Gomes & Sousa 2133* (COI, K). MAPUTO: Manhiça, vale do Incomati, 26 Mar. 1979, *de Koning 7353* (K, LISC, LMA); Marracuene, between the Incomati pontoon and Lake Pati, 40 km from the pontoon, 24 Mar. 1954, *Barbosa & Balsinhas 5450* (LISC, LMA); Vila Luisa, Macaneta, 18 Apr. 1974, coastal dune, *Balsinhas 2699* (LMA, PRE); Marracuene, ao km 12 de Vila Luiza para Manhica, 6 Feb. 1969, *Correia & Marques 591* (WAG). SOUTH AFRICA. TRANSVAAL: 22.31 (Pafuri), Kruger National Park, Klapperfontein, 21 Jan. 1953 (CA), *van der Schijff 1858* (PRE); 23.30 (Tzaneen) Hans Merensky Nature Reserve, mopane veld in damp earth along sloot, 11 Feb. 1971 (DA), *Oates 371* (PRE); Merensky Nature Reserve, waterlogged clay loam in vlei, 2,000 ft., 15 Mar. 1977, *Zambatis 737* (PRE); 24.30 (Pilgrims Rest), Shilouvane, Jan. 1919 (AB), *Junod 4139* (G, M, PRE); Shilouvane Plaine, s.d., '*L. junodii* N. E. Br.' *Junod 736* (G, K); 10 m N of Abel Erasmus Pass, grass in bushveld, 16 Dec. 1964 (DA), *Mauve 4326* (K, PRE); 24.31 (Acornhoek), farm Grootdraai, stony flats, 1,500 ft., 15 Nov. 1973 (AA), *Zambatis 543* (MO); Klaserie, farm Sark, seasonal seep in sandy clay, 28 Jan. 1982 (AC), *Zambatis 1345* (PRE); Kruger National Park, 25 Feb. 1953 (AD), *van der Schijff 2365* (PRE); Pumbe, Satara, sandy soil, Mar. 1967 (BB), *van Wyk 4783* (PRE); Manyeleti Game Reserve, clay, 400 ft., 9 Mar. 1977, *Bredenkamp 1762* (PRE). ZIMBABWE. VICTORIA: Bikita District, Burchenough-Fort Victoria road, 16 May 1962, *Noel 2427* (K, LISC, SRGH); near Morgenster Mission, 17 Mar. 1958, *Leach 8219* (SRGH); Kyle National Park, clay slope above granite outcrop, 9 Feb. 1972, *Gibbs Russel 1465* (SRGH); Kyle Dam, shade in gully by granite outcrop, 8 Jan. 1972, *Gibbs Russel 1452* (SRGH); Belingwe, near the Mnene road, among rocks, *Norlindh & Weimarck 5202* (BR, PRE, S, SRGH).

10. Lapeirousia sandersonii Baker, Handbk. Irideae 169. 1892; Fl. Cap. 6: 95. 1896; Fl. Trop. Africa 7: 352. 1898, excl. specimens cited. van Druten, Fl. Pl. Africa 31: 1226. 1956. Letty, Wild Flowers of the Transvaal 77, t. 37. 1962. TYPE: South Africa: Transvaal, *Sanderson s.n.* (lectotype, K, here designated); Rhenosterpoort, *Nelson 402* (syntypes, K, PRE); Transvaal, without precise locality, *Todd 20, 21* (syntype, K). As no type was indicated in the protologue, a lectotype has been selected from among the four specimens from South Africa cited in *Flora Capensis* (1896). None of the several more from tropical Africa cited by Baker (1898) are this species. The Sanderson collection from the Transvaal chosen as the lectotype is already so annotated in the Kew Herbarium (by N. E. Brown ?). Figure 11.

Lapeirousia bainesii var. *breviflora* Baker, J. Linn. Soc. Bot. 16: 156. 1856, nom. nud. (no specimen cited, but *Nelson 402*, see above, is so annotated).

Plants 18–35 cm high. *Corms* 2.5–3 cm diam., tunics dark brown, coriaceous internally, decaying somewhat irregularly into vertical segments, seldom becoming fibrous and never reticulate. *Cataphylls* usually 2, dark brown, the inner one reaching to shortly above ground level, the outer much shorter. *Leaves* 2–4, ± linear, 2–3 mm wide, firm to rigid, the midrib and lateral veins fairly prominent and closely set, the lowermost longest and usually exceeding the inflorescence, the upper leaves progressively shorter. *Stem* compressed, 2-angled to winged below, triangular above the branches and often lightly winged on the angles. *Inflorescence* much branched, sometimes intricately so, the branches ± divaricate but unequal and a main axis

usually evident, the ultimate branches 1–2(–3)-flowered; *bracts* (4.5–)5–8(–10) mm long, herbaceous with brown tips in bud, often flushed purple, becoming scarious throughout in later flower and brown almost entirely. *Flowers* zygomorphic, blue to violet, the lower 3 tepals each with a deep red to purple and white spear-shaped nectar guide in the lower midline; *perianth tube* 15–18(–20) mm long, slender, but slightly wider in the upper 2–3 mm; *tepals* subequal, 10–11 mm long, lanceolate, 3–3.5 mm wide, the upper held apart from the others and reflexed, the lower 3 joined for about 1 mm and forming a lip, when fully open all held in ± the same nearly horizontal plane. *Filaments* unilateral, ± erect, ca. 5 mm long, exserted 3 mm from the tube; *anthers* parallel and contiguous, 3–4 mm long, purple; pollen pale yellow. *Ovary* ovoid, ca. 2 mm long, *style* dividing near the apex of the anthers, the branches simple or divided for a short distance, ca. 1.5 mm long. *Capsules* depressed globose, ca. 5 mm diam., 4–5 mm long; *seeds* nearly globose, ca. 2 mm diam. *Chromosome number* $2n = 10$.

Flowering time. December to April.

Distribution and habitat. *Lapeirousia sandersonii* is native to the interior of eastern Botswana and the adjacent part of South Africa, where it occurs in the relatively dry northern and western Transvaal and the northern Cape (Fig. 11). It appears to be most common in the Pretoria and Rustenburg areas of the Transvaal, and, according to the collection record, relatively rare in the northern Transvaal and Botswana. The easternmost records from the cool, high, well watered Dullstroom, Belfast, and Middleburg areas of the eastern Transvaal are surprising in view of the rest of the range in semiarid country, but the eastern populations differ in no significant way from those occurring further west. The habitat is always rocky, and usually well drained, such as hill slopes, ridges and summits. Corms are seldom collected, which probably reflects the difficulty in extracting them from rocky ground.

Diagnosis and relationships. Clearly a member of the *Lapeirousia erythrantha* complex, *L. sandersonii* has the repeatedly branched, pseudopaniculate inflorescence and blue-violet flowers that characterize most tropical African species of *Lapeirousia*. It can be distinguished from the related *L. erythrantha* by its longer perianth tube 15–20 mm long, and by its usually highly ramified and divaricately branched inflorescence with 1–2 (–3) flowers on the major terminal branches. *Lapeirousia sandersonii* is most easily confused with occasional longer-tubed forms of *L. erythrantha* that occur in eastern Zimbabwe and Malawi, but these plants have shorter bracts 4–6 mm long, and less-branched inflorescences with 3–5 flowers per main terminal branch. These long-tubed forms of *L. erythrantha* are particularly variable and consist of plants with tubes ranging from 12 to 15 mm. A population from near Dedza in central Malawi that is particularly variable for perianth tube length has a chromosome number of $2n = 12$ exactly corresponding to that in surrounding populations of *L. erythrantha* and unlike the karyotype of subsp. *sandersonii*, which has $2n = 10$ (Goldblatt, 1990b).

Also easily confused with *L. sandersonii* is *L. masukuensis* of the eastern Transvaal, southeastern Zimbabwe, and Mozambique. This species has flowers with a particularly long perianth tube, typically 20–25 mm long, soft-textured leaves, coarsely fibrous to reticulate outer tunic layers, and 5–9 flowers per major terminal inflorescence branch. The two have often been confused, and the later name, *L. masukuensis*, has not been used in herbaria. It seems distinct from *L. sandersonii*, not only in several morphological characters but also in the lowland distribution, from 2,000 ft. to near sea level, and preference for wet sites such as vleis, seeps, or seasonally waterlogged flats.

A few collections of *Lapeirousia* from the Waterberg in the western Transvaal broadly resemble *L. sandersonii* in habit, leaf, and corm, but the flowers have a perianth tube 10–12 mm long (e.g., *Werdermann & Oberdieck 1640*). The short perianth tube in *L. sandersonii* from this area is puzzling. These plants are indicated by an asterisk in the exsiccatae.

History. Collected first by John Sanderson, probably in 1852 when he traveled to Rustenberg and the Magaliesberg on his only journey to the Transvaal, *Lapeirousia sandersonii* first appeared in the literature as "*L. bainesii* var. *breviflora*," a nomen nudum of J. G. Baker (1876). Baker subsequently described *L. sandersonii* in 1892, and it was so treated in *Flora Capensis* and *Flora of Tropical Africa*. W. Marais (pers. comm.) suggested that it be assigned infraspecific status in *L. erythrantha* although he preferred varietal rank.

Additional specimens examined (unusual short-tubed forms are indicated by an asterisk [*]). BOTSWANA. KGATLENG: 24.25 (Gaborone) near Molepolole, shale, 15 Apr. 1930 (BC), *van Son s.n.* (PRE 28664); W of Gaborone Dam (DB), 1976, *Mott 928* (SRGH, UCBG). NGWAKETSE: 25.25 (Mafeking) 6 mi W of Kanye, 12 Feb. 1971 (AB), *van Rensburg B4226* (PRE). SOUTH

AFRICA. CAPE: 26.24 (Vryburg) Moshesh near Mosita, ironstone koppie, 10 Apr. 1945 (BB), *Brueckner 470* (K, PRE); Vryburg, 5 Feb. 1948 (DC), *Rodin 3501* (K, MO, P, PRE, S); 27.23 (Kuruman) Bathlaros, Apr. 1921 (AC), *Silk 231* (K); 7 mi. SW of Kuruman, *Wisura 2003* (NBG). TRANSVAAL: 22.29 (Waterpoort) Zoutpansberg, 1 mi. from Dandy farm, road to Sand River, S slopes in rocky outcrop, 3 Apr. 1957 (DC), *Meeuse 10212* (K, M, PRE, SRGH); farm Thornhill 743, red sand in riverine woodland, 18 Mar. 1985 (DD), *Raal 434* (PRE); 22.30 (Messina) Louis Trichardt, farm Rietbok 226, among rocks in montane scrub forest, 1,476 m, 25 Mar. 1982 (CC-CD), *Venter 7812* (PRE); 23.27 (Ellisras) *Waterberg, 67 mi. N of Vaalwater on Beauty road, 3 Feb. 1983 (DB), *Reid 656* (PRE); *Waterberge, between Groothoek and Vaalwater, 1,000 m, 6 Jan. 1959 (?), *Werdermann & Oberdieck 1640* (B, BR, GH, K, MO, PRE, WAG); 24.28 (Nylstroom) *Vlakfontein, 3 mi. N of P. O. Palala, 29 Jan. 1960 (BC), *Codd 9975* (PRE); Sterkrivier Nature Reserve, rocky slope in mixed woodland, below slabs of bedrock, 13 Mar. 1973 (BD), *Jacobsen 2794* (PRE); koppie 19 km from Warmbaths on Kwaggasnek road, W slope, 13 Feb. 1981 (CC), *Herman 227* (PRE); 24.30 (Pilgrims Rest) 5.3 m from Burgersfort on Steelpoort rd., 2,500 ft., 14 Mar. 1953 (CB), *Story 4067* (GRA, K, PRE, SRGH); 25.26 (Zeerust) Zeerust, 28 Jan. (CA), *Thode A1503* (GH, K); Zeerust, Feb. 1912, *Jenkins TM11660* (K, PRE); 15 m E of Swartruggens, bushveld on ridges (DB), 14 Feb. 1956, *Acocks 18747* (K); 15 mi. E of Swartruggens on the Rustenburg road, 25 Feb. 1947, *Sidey 83* (S); Koster, among rocks in kloof, 1 Apr. 1929 (DD), *Gilmore 1915* (G); 25.27 (Rustenberg) Rustenberg, 4,000 ft., stony hillside near town, July 1904 (fl & fr) (CA), *Pegler 1108* (GRA, K, PRE, SAM); 22 m W of Rustenberg, 14 Feb. 1956, *Leistner 539* (K, PRE); Rustenberg, Tierkloof, moeras by wildreservaathek, 13 Mar. 1976, *Venter 654* (K, MO, PRE, SRGH, WAG); Rustenberg Nature Reserve, rocky hillsides in grassland, 25 Feb. 1970, *Jacobsen 745* (PRE); 16 km from Palala on road to Bamboeskloof, 9 Mar. 1978 (CC), *Germishuizen 735* (PRE); Breedtsnek, grass on open mountain top, 7 Apr. 1939 (fr) (CD), *Connell 42* (PRE); Brits, Silikaatsnek, top of poort in shallow sand over quartzite (DB), *Codd 736* (PRE); 14 Feb. 1946, *Story 810* (PRE); Krugersdorp, Jack Scott Nature Reserve, 2 Feb. 1961 (DC), *Wells 2305* (K); 25.28 (Pretoria) Hornsnek Pass, Magaliesberg, W side, S slope in grassland, 31 Jan. 1983 (CA), *Perry 2017* (NBG); Hornsnek, 12 km W of Pretoria, 12 Jan. 1956, *Schlieben 7751* (B, BR, G, HBG, K, M); Hornsnek, light shade on summit among rocks, 10 Feb. 1951, *Prosser 1604* (K, NBG, PRE); N slopes of Magaliesberg, 25 Mar. 1945, *Mogg s.n.* (K, M, PRE 27329, S, SRGH); The Willows, Pretoria, 9 Mar. 1906, *Burtt Davy 5333* (GRA, K), *1703* (K); Cullinan, farm Vaalwaterkrans, 25.2 km from Pretoria on Roodeplaat Dam road, 28 Feb. 1980 (CB), *Retief & Herman 159* (MO, PRE); Pienaarspoort, 17 mi. E of Pretoria, 20 Feb. 1959, *Brent 138* (K, PRE); Tierpoort Vakansieoord, E of Pretoria, sandstone rock crevices and slopes, 8 Mar. 1977 (CD), *van Jaarsveld 1870* (NBG); Donkerhoek, 20 mi. E of Pretoria, 19 Mar. 1959, *Codd 9908* (K, PRE); 19 Mar. 1959, *Letty 428* (K, PRE); Donkerhoek, rocky koppie, 11 Mar. 1943, *Verdoorn 1908* (PRE); Premier Mine, Jan. 1919 (DA), *Rogers 22415* (K, P, SAM); June 1921, *Rogers 24146* (B, BR, G, GRA, K, LISC, MO, P, S, SAM); Renosterkop, Bronkhorstspruit District, 7 Feb. 1932 (DB), *Young 2116* (K, PRE); farm Valsspruit, 19 km N of Bronkhorstspruit, 10 Feb. 1984, *Crosby 64* (PRE); 25.29 (Witbank) Loskop Dam, Nooitgedacht, shallow ground on summit, 9 Feb. 1967 (AD), *Theron 1214* (PRE); 5 mi. W of Middelburg, 30 Jan. 1929 (CD), *Hutchinson 2716* (K, PRE); Botsabelo, Renosterpoort, mountain summit, Mar. 1878, *Nelson 402* (K, PRE); 25.30 (Lydenburg) hills above Dullstroom, 23 Feb. 1937 (AC), *van der Merwe 1255* (B, K, PRE); Dullstroom, among dolerite rocks on farm Valleispruit, 6,500 ft., 30 Jan. 1933, *Galpin 13369* (K, P, PRE); farm Onverwacht 99, E aspect on shallow stony ground, s.d., *Engelbrecht s.n.* (PRE 664971); Belfast, Feb. 1909 (CA), *Doidge 4800* (K); 26.27 (Potchefstroom) Dassiesrand, Potchefstroom, 23 Mar. 1940 (CA), *van der Westerhuizen 1114* (PRE). WITHOUT PRECISE LOCALITY. SOUTH AFRICA: Transvaal, Oct. 1869, *Buchanan 20, 21* (or Todd sub Buchanan); Jan. 1924, *Rogers 28286* (G, K) (as Natal, Weenen, Culvers 6,000 ft., which is almost certainly incorrect).

11. Lapeirousia gracilis Vaupel, Bot. Jahrb. Syst. 48. 548. 1912. Sölch, Prod. Fl. Südwestafrika 155: 9. 1969. TYPE: Namibia: Great Namaqualand, Doorns, dolomite, 1,450 m, Mar. 1907, *Range 292* (holotype, B; K (photo), M, fragment). Figure 12.

Plants (12–)15–30 cm high, often fairly slender, but occasionally robust, few- to several-branched. *Corm* 12–18 mm at the widest diameter, narrowly campanulate, tunics light brown, coriaceous, outermost layers becoming coarsely fibrous, the fibers extending upward as short spines. *Leaves* 2–3 (–4), the lowermost inserted just below the ground, the lower or second leaf usually the largest, the upper decreasing in size, becoming bractlike, linear to narrowly lanceolate, 3–5(–8) mm at the widest, the longest about as long or somewhat longer than the inflorescence, somewhat thickened around the midvein, a second vein on either side of the midvein also sometimes evident. *Stem* erect below, branching ± divaricately and the branches ascending but flexed to become ± erect at the base of the flowers, 2-angled and winged below the first branch, 3-angled and winged above, the wings often prominent. *Inflorescence* ± paniculate or the branching sparse, the ultimate branches short spikes of (1–) 2–6 flowers; *bracts* (4–)6–7 mm long, herbaceous below, becoming ± membranous above, sometimes flushed purple, sometimes membranous and completely dry before anthesis, then usually transparent or with fine brown veins, subequal or the inner or outer larger. *Flowers* zygomorphic, white to pale blue or mauve, the lower 3 tepals yellow at the base and outlined distally by a dark violet margin, and each marked with a purple median streak or spot, occasionally one or more of the lower tepals with a small median toothlike callus in the midline, lightly fragrant; *perianth tube* cylindric, slightly

FIGURE 12. Morphology and distribution of *Lapeirousia gracilis*. Habit and corm × 0.5; single flower full size; details of stamens and style × 2. (Drawn by J. C. Manning.)

curved outward at the apex, (21–)25–38 mm long; *tepals* nearly equal in size, lanceolate, ca. 10 mm long, 4–5 mm wide, the margins lightly undulate, the lower 3 closer together, apparently forming a lip, the uppermost held apart and nearly erect to reflexed, rarely the lower 3 tepals each with a short median toothlike callus. *Filaments* unilateral, exserted for ca. 2 mm; *anthers* parallel and contiguous, ca. 5 mm long, pale lilac; pollen cream. *Ovary* obovoid, ca. 2 mm long, *style* arching behind the filaments, dividing near the apex of the anthers, branches 1.5–2 mm long, forked for ca. 0.5 mm, ultimately recurving. *Capsules* ± globose, obtusely trigonous, 4–5 mm long, 5–6 mm diam.; *seeds* globose to weakly angular, ca. 2 mm diam., dark brown. *Chromosome number* $2n = 12$.

Flowering time. Late January to April.

Distribution and habitat. *Lapeirousia gracilis* is endemic to Namibia, where it occurs in a relatively broad band along the west central part of the country (Fig. 12). It occurs in rocky sites or sometimes on sandy flats; especially in more arid areas it is often associated with springs or other places where additional water supplements the sparse rainfall. The range of *L. gracilis* extends from the Fish River Canyon in the south to the Hoanib River in the Kaokoveld in the north. Flowering normally takes place at the end of summer, mostly in February and March but sometimes as late as May. An October-blooming collection, *Craven 1341*, from the Brandberg is difficult to explain; perhaps it indicates an unusual rainfall pattern in a particular year. The spring-blooming specimens do not appear to differ from those collected flowering in the summer.

Diagnosis and relationships. The slender perianth tube 25–38 mm long, white to pale blue flower color, and comparatively slender habit make most specimens of *Lapeirousia gracilis* easy to recognize. It most closely resembles *L. bainesii* and *L. otaviensis*, both of which have similarly long-tubed flowers. *Lapeirousia bainesii* has white to pale pink flowers with dark red to brown markings and a tube 35–47 mm long. It also has a

more robust habit and longer floral bracts 7–12 mm long; the highly ramified inflorescence has only 1(–2) flowers per ultimate branch. Occasional robust specimens of *L. gracilis* must be examined carefully to avoid confusing them with depauperate *L. bainesii*.

Confusion with *Lapeirousia otaviensis* is more likely since this species, like *L. gracilis*, has an inflorescence with the main terminal branches bearing 2–5 flowers. The flowers and bracts of *L. otaviensis* are larger and the perianth tube slightly longer than in *L. gracilis*. The latter typically has short and transparent floral bracts 4–7 mm long, a useful guide when flower size is intermediate and perianth color is unknown. Sölch (1969) distinguished *L. gracilis* by its shorter perianth tube and more slender habit but not by flower color, which he described as white in both this and *L. bainesii*. This is generally incorrect for *L. gracilis*; although the flowers fade after drying and appear white, I have seen few collections describing the living flower as white and several that indicate shades of blue, evidently the more common perianth color in *L. gracilis*.

Phylogenetic relationships are difficult to postulate with confidence in *Lapeirousia*, but it seems plausible that *L. gracilis*, *L. bainesii*, and *L. otaviensis* are immediately allied, sharing the derived features of pale-colored flowers having an extended perianth tube and pale, reticulate corm tunics (Table 3). The chromosome number of *L. gracilis*, $2n = 12$, and bimodal karyotype (Goldblatt, 1990b) differ from that in *L. otaviensis* and *L. bainesii*, which have $2n = 10$ or 6 and nonbimodal karyotypes.

History. Discovered in 1907 by the German geologist Paul Range near Doorns in southern Namibia, *Lapeirousia gracilis* was described in 1912 by Vaupel. It was for many years poorly known but botanical exploration in the 1960s and 1970s has revealed a coherent distribution pattern.

Additional specimens examined. NAMIBIA. KAOKOVELD: 19.12 (Hoanib Mouth) Hoanib River valley, ca. 20 km inland, rocky hills among boulders, 20 Apr. 1985 (BD), *Moss & Jacobsen K311* (PRE, WIND). OMARURU: 21.14 (Uis) Brandberg, 17 Oct. 1981 (AB), *Craven 1341* (WIND); Brandberg, Orabeswand, 2,000 m, 6 Apr. 1964, *Nordenstam 3666* (M, S). KARIBIB: 21.15 (Karibib) farm Klein Spitzkoppe, coarse granitic sand, W slopes and below the summit, 23 Feb. 1965 (CC), *Giess 8496* (B, K, M, MO, PRE, S, WAG, WIND); 22.15 (Trekkopje) farm Tsabichab, cracks in marble rock around spring, 19 May 1973 (BA), *Giess 12744* (K, M, MO, S, WIND); 22.16 (Otjimbingwe) Namibrand, Karibib, Otjosandu, 1 Mar. 1963 (AA), *Seydel 3419* (B, C, G, GH, K, MO, S, SRGH, WAG, WIND). REHOBOTH: 23.16 (Nauchas) farm Weisenfels, 11 Mar. 1953 (AD), *Walter & Walter 1675* (B, WIND); 23.17 (Rehoboth) Buellsport, flats, Mar. 1949 (?), *Strey 2700* (PRE). MALTAHOHE: 25.16 (Helmeringhausen) farm Chamchawib, 23 Jan. 1974 (DB), *Giess & Robinson 13255* (K, M, MO, PRE, WAG, WIND); farm Saraus, lower pass, in black limestone, 18 Feb. 1963, *Giess et al. 5229* (M, MO, PRE, WIND). MARIENTAL: 24.17 (Mariental) farm Haribes, dry sterile vlei, 1 Mar. 1963 (DA), *Giess et al. 5571* (M, PRE, WIND); 27 Apr. 1956, *Volk 12105* (M, WIND); 25.17 (Gibeon) Asab, hard clay along the railtracks, May 1913 (BD), *Dinter 3061* (SAM); 13 Mar. 1988, *Goldblatt & Manning 8770* (K, MO, NBG, PRE, S, WIND). KEETMANSHOOP: 26.18 (Keetmanshoop) Spitzkoppe, 7 Apr. 1984 (AD), *Craven 1666* (WIND). WARMBAD: 27.17 (Chamaites) Fish River Canyon, river camp, 30 Mar. 1953 (DA), *Walter & Walter 2263* (B, WIND); Fish River Canyon, middle plateau, 23 Feb. 1963, *Leipert 4221* (WIND); Fish River Canyon Reserve, edge of the canyon, 12 May 1965, *Meyer 4* (M, WIND); Seeheim, Apr. 1900, *Schafer 383* (B). WITHOUT PRECISE LOCALITY: NAMIBIA: Quartel/Rehoboth, 10 Apr. 1911 (fr), *Dinter 2152* (SAM).

12. Lapeirousia otaviensis R. Foster, Contr. Gray Herb. 127: 45–46. 1939. (*Lapeirousia bainesii* sensu Sölch, Prod. Fl. Südwestafrika 155: 8. 1969.) TYPE: Namibia: Auros farm near Otavi, 11 Feb. 1925, *Dinter 5577* (holotype, GH; isotypes, B, G, PRE, SAM, Z (3)). Figure 13.

Plants 30–55 cm high, repeatedly branched. *Corm* 2–2.5 cm diam., tunics light brown, coriaceous, becoming reticulate and coarsely fibrous with age, sometimes ultimately finely fibrous. *Cataphylls* 2, membranous, the inner reaching to shortly above the ground. *Leaves* 4–7, ± linear (to narrowly lanceolate), gray-green, only the midrib prominent, the lower 2–4 basal and longest, 5–9 mm wide, exceeding the inflorescence by 5–10 cm; upper leaves cauline and decreasing in size above, those subtending the branches becoming bractlike. *Stem* weakly compressed below, triangular in the middle part and rectangular above, the angles lightly winged, the main axis straight, branches diverging at 45–80°. *Inflorescence* a ± corymbose pseudopanicle, the main terminal branches with (1–)3–5 flowers in a short spike; *bracts* herbaceous, lanceolate and acute, often flushed red above, becoming dry apically, usually quite dry when the flowers have wilted, (7–)8–11 mm long, the inner often longer than the outer. *Flowers* zygomorphic, white to cream, sometimes flushed pale lilac, rarely purple, the lower 3 tepals each marked with violet streak in the midline and with darker double purple to red lines near the base, rarely the upper tepals with a pale purple median line, unscented and opening in mid morning; *perianth tube* 40–45 mm long, straight, very

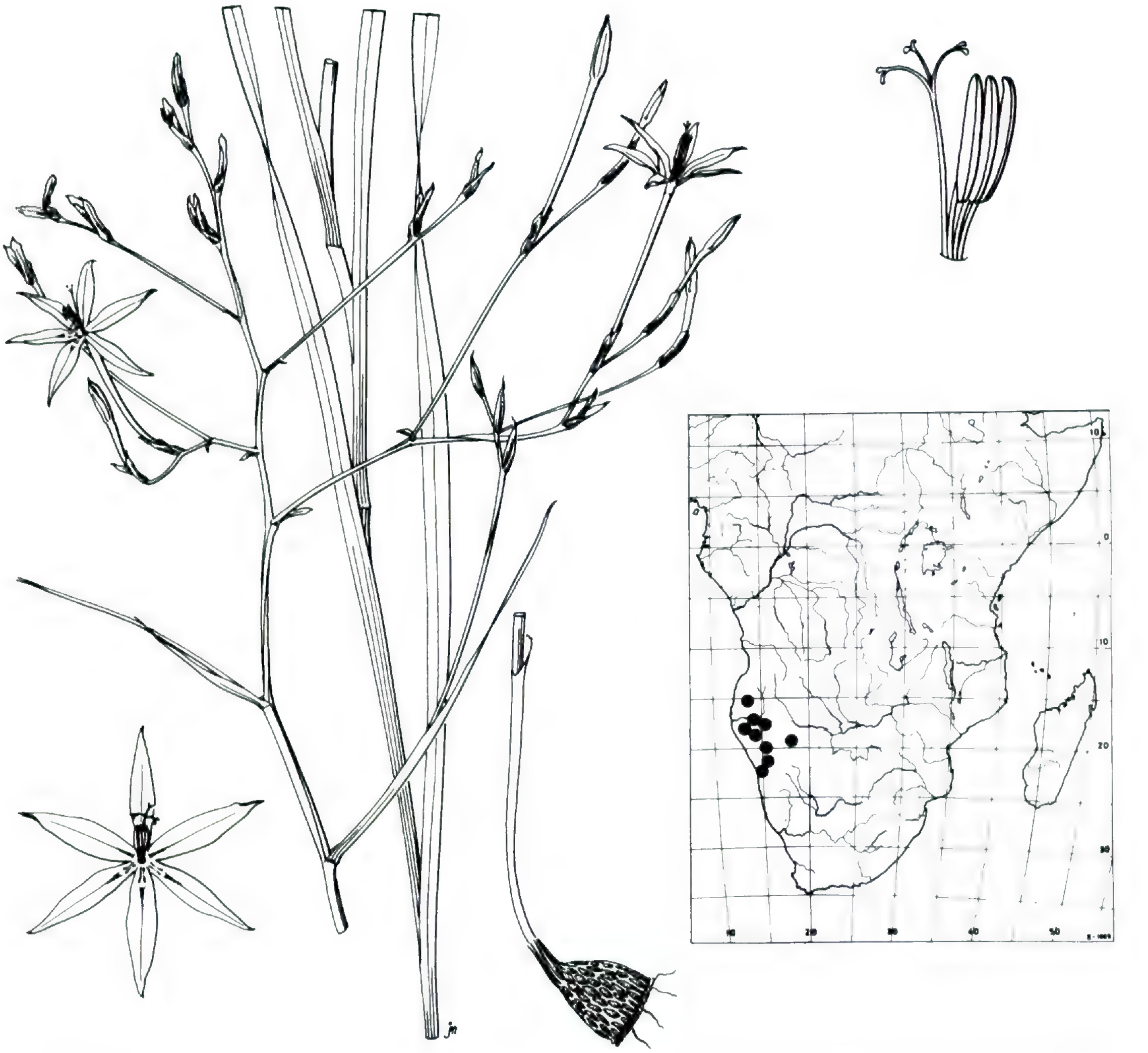

FIGURE 13. Morphology and distribution of *Lapeirousia otaviensis*. Habit × 0.5; single flower full size; details of stamens and style × 2.5. (Drawn by J. C. Manning.)

gradually flared from the base, about 1.2 mm diam. below, 2.2 mm diam. at the mouth; *tepals* subequal, lanceolate, widest in the middle, the margins straight, 15–19 mm long, 4–5 mm wide, spreading almost at right angles to the tube, the uppermost slightly larger than the others, weakly to strongly acute. *Filaments* unilateral, exserted for 4–5 mm from the tube, white; *anthers* parallel and contiguous, 5–6 mm long, gray-purple; pollen white. *Ovary* ± ovoid, ca. 2 mm long; *style* nearly straight, lying behind the filaments, the branches usually dividing at (or to 3 mm beyond) the anther apices, branches ca. 2 mm long, forked for ⅓–½ their length, diverging but barely or not at all recurved. *Capsules* globose trigonous, ca. 7 mm long; *seeds* not known. *Chromosome number* $2n = 10$.

Flowering time. February to April.

Distribution and habitat. Of relatively restricted distribution, *Lapeirousia otaviensis* occurs in a wide arc from the Erongo Mountains in western Namibia through the hills south of Etosha Pan to the Otavi Hills in the northeast and locally also in southern Angola (Fig. 13). It is apparently confined to rocky outcrops, usually growing in granite, but in the Otavi Hills it occurs on local shale outcrops, not in the dolomite that predominates in this area.

Diagnosis and relationships. The large flower with a long perianth tube 4–5 cm long, white to lilac perianth with lanceolate tepals, and the ultimate branches of the inflorescence having up to five flowers (and rarely fewer than two) distinguish *Lapeirousia otaviensis*. It has often been confused in herbaria with the apparently related

L. bainesii and was even regarded as identical to this species by W. Marais (pers. comm.; Geerinck et al., 1972), under the name *L. erythrantha* var. *bainesii*. *Lapeirousia otaviensis* and *L. bainesii* both merit specific status. They can be separated by a series of characters, and they do not intergrade with each other or with any of the forms of *L. erythrantha* and its close allies. *Lapeirousia bainesii* has flowers with a slightly shorter perianth tube 30–40 mm long, this often purplish in color, and has more or less clawed, white tepals with undulate margins. The inflorescence of *L. bainesii* branches divaricately, and the ultimate branches have one or rarely two flowers. *Lapeirousia otaviensis* is restricted to rocky sites of granite or shale, whereas *L. bainesii* occurs in deep hard sand in level savanna or bushveld.

An interesting color variant of *Lapeirousia otaviensis* occurs on the plateau and higher parts of the Erongo Mountains (*Craven & Craven 115*; *Lavranos 22693*). This has purple flowers in contrast to the white or pale lilac elsewhere. Apart from the perianth color, there seem to be no significant differences between this and the more widespread color form.

A collection from southern Angola made in 1909, *Pearson 2738*, is assigned here, but the poorly preserved plants are either depauperate or possibly belong to the related *L. gracilis*. The perianth tube is 35–48 mm long, within the range of variation encountered in *L. otaviensis*. The brown-tipped bracts are 7–9 mm long, which corresponds with *L. otaviensis* but is also in the upper range for *L. gracilis*. The latter is centered in southern to west central Namibia, whereas *L. otaviensis* occurs across northern Namibia so that the latter determination is phytogeographically the more likely.

History. Although first collected in 1879 in "Damaraland" by Ture Een, an early botanical explorer in Namibia, *Lapeirousia otaviensis* was described in 1939 by the American R. C. Foster from a gathering made in 1925 by Dinter at Auros farm near Otavi. This was the first collection of *L. otaviensis* to be distributed widely to herbaria. It seems to have been recognized as a distinct species by accident, as Foster compared it to the very different, short-tubed *L. avasmontana* in the protologue. The reason for this is obscure and may have been because he had misidentified material of the latter. Apparently Foster was unaware at this time of the similarities that *L. otaviensis* shared with *L. bainesii*, and with which *L. otaviensis* became confused later. In the *Prodromus Flora Südwestafrika* (Sölch, 1969) *L. otaviensis* and *L. bainesii* were treated as conspecific and distinguished in the key by having several-flowered ultimate inflorescence branches. Sölch reserved the name *L. vaupeliana* Dinter for what is here called *L. bainesii*. The type material of *L. vaupeliana* has all the characters of *L. bainesii*, including one-flowered ultimate inflorescence branches.

Additional specimens examined. ANGOLA. HUILA: damp sandy places near Monino, Humpata Pass, 3 Apr. 1909, *Pearson 2738* (K). CUNENE: top of Ruacana Falls, N bank, crevices in moist springs, 30 Apr. 1967, *Rycroft 2443* (NBG, WIND). NAMIBIA. KAOKOVELD: 17.12 (Posto Velho), granite slope at Ombepera, rock crevices, corms edible, 10 Apr. 1957 (BD), *de Winter & Leistner 5481* (B, K, M, PRE, WIND); Orumana, stony flats below dolomite ridge, 20 Mar. 1974 (BD), *Merxmüller & Giess 30407* (M, PRE, SRGH, WAG, WIND); Kunene River banks, Mar. 1925, *Barnard 1381* (SAM). KARIBIB: 21.15 (Karibib), W edge of the Erongo Mountains above farm Ameib KAR 60, 27 Mar. 1976 (DC), *Craven & Craven 115* (WIND); Erongo Plateau, among granite boulders, 1985, *Lavranos 22693* (E, K, M, MO, P, S); 22.15 (Trekkopje) Okongava, granite slope on Kalkberg, 4 Feb. 1934 (BB), *Dinter 6962* (B, BM, G, HBG, K, M, PRE, S, WIND, Z). OMARURU: 20.15 (Ohjihorongo) 90 km from Omaruru on the road to Fransfontein, Table Mountain, by Ozondati, 11 Apr. 1968, *Wanntorp & Wanntorp 840* (K, S). OUTJO: 19.14 (Kamanjab) 8 km N of Kamanjab-Nord, granite domes, 18 Mar. 1974 (DB), *Merxmüller & Giess 30392* (K, M, PRE, WAG, WIND); Kamanjab, dry granite hills in rock crevices, 2 Mar. 1957, *de Winter & Leistner 5132* (B, K, M, PRE, WIND); Kamanyab, Mar. 1925, *Thorne s.n.* (SAM 31741); 20.16 (Otjiwarongo) Paresis Mts. (AD), *Barnard 201* (SAM). GROOTFONTEIN: 19.17 (Tsumeb) farm Auros, slopes behind the farm house in grassy sites, 1,800 m, 10 Mar. 1974 (DA), *Merxmüller & Giess 30186* (M, PRE, WAG, WIND); Auros Farm, shale hills near the farm house, 21 Mar. 1988, *Goldblatt & Manning 8837* (E, K, M, MO, NBG, PRE, S, WAG, WIND). WITHOUT PRECISE LOCALITY: NAMIBIA: Damaraland, 1879, *Een s.n.* (BM); Kunene River banks, Mar. 1925, *Barnard 1381* (SAM).

13. Lapeirousia bainesii Baker, J. Bot. 14: 338. 1876; Handbk. Irideae 170. 1892; Fl. Trop. Africa 7: 352. 1898. Sölch, Prod. Fl. Südwestafrika 155: 8. 1969 (but applied to *L. otaviensis*). TYPE: Botswana: Kobe Pan (inter Koobie et N Shaw valley), *Baines s.n.* (lectotype, annotated as "TYPE" by N. E. Brown, and confirmed here as lectotypified, K); South Africa. Transvaal: *Todd s.n.* (syntype, K—as *Todd 19*). Figure 14.

Lapeirousia vaupeliana Dinter, Feddes Rep. 18: 436. 1922. Sölch, Prod. Fl. Südwestafrika 155: 8. 1969. TYPE: Namibia: Gameros (cult. Okahandja), *Dinter 3087* (lectotype, B, designated by Sölch in 1959); Gameros, *Dinter 2787a* (syntype, SAM); Okakeua u. Okanjatu, *Dinter 3374* (syntype, SAM).

Plants 30–60 cm high, usually repeatedly branched. *Corm* 13–20 cm diam., tunics middle

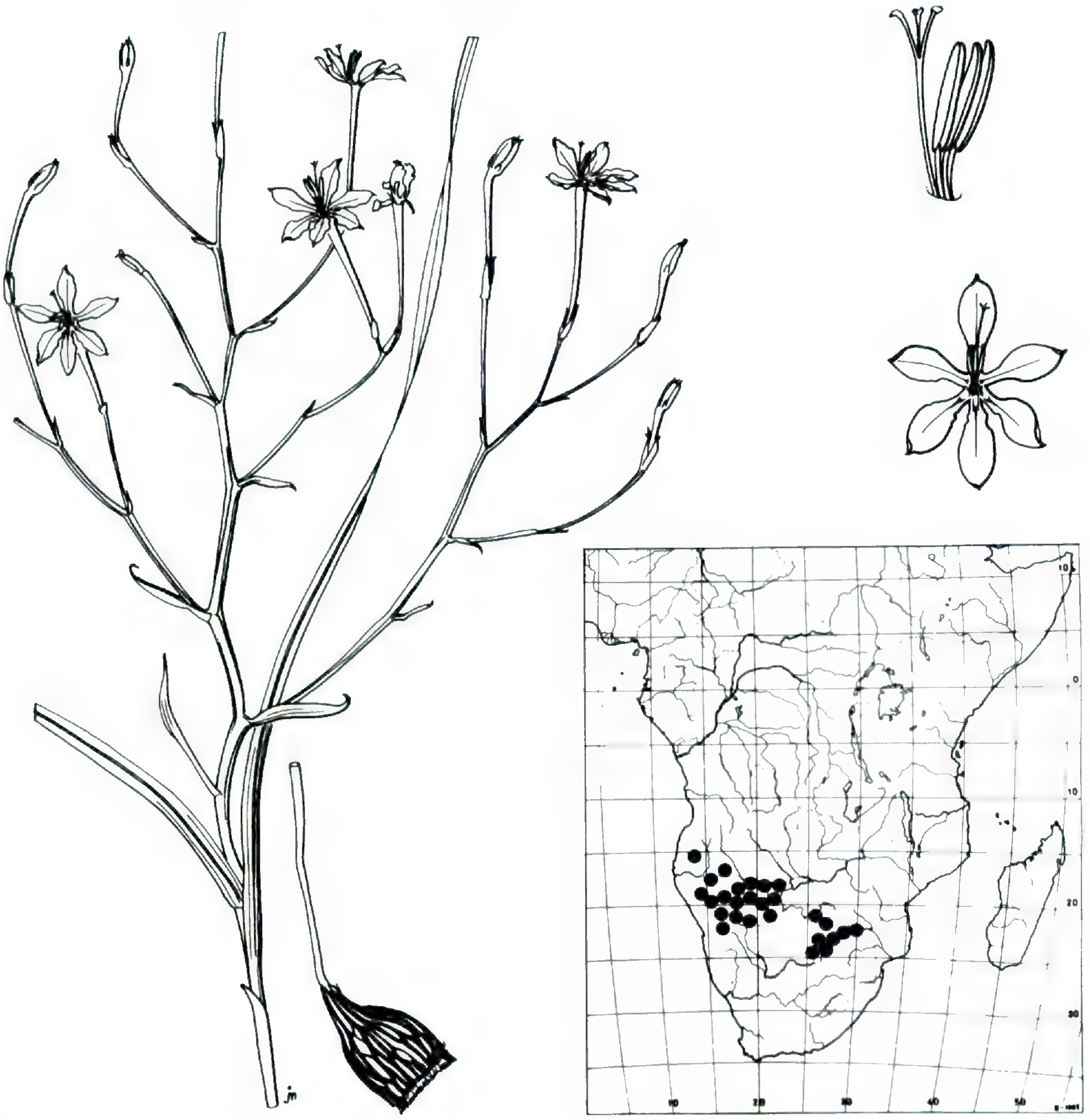

FIGURE 14. Morphology and distribution of *Lapeirousia bainesii*. Habit and corm × 0.5; single flower full size; details of stamens and style × 2. (Drawn by J. C. Manning.)

to dark brown, coriaceous to cartilaginous internally with the veins sharply outlined, decaying to become ± fibrous, the fibers wiry and coarse. *Cataphylls* 2, pale and membranous, the inner reaching 2–4 cm above the ground. *Leaves* narrowly lanceolate to linear, glaucous, 5–7 mm wide, usually slightly longer than the inflorescence, midrib prominent and a lateral vein on either side of the midvein evident. *Stem* compressed and 2-winged below, 3–4-angled and winged above, the wings sometimes slightly crisped to serrulate. *Inflorescence* a pseudopanicle, the branching divaricate, ultimate branches with 1(–2) flowers, the axes angularly trigonous; *bracts* 7–10(–12) mm long, herbaceous below, dry before anthesis, becoming membranous, dry and light brown especially above and the apices often darker brown, the inner slightly larger than the outer. *Flowers* zygomorphic, white to cream, sometimes flushed pale pink, the tube pale purple, the lower 3 tepals each usually marked with a red to brown streak in the lower half and a dark mark at the base, the top of the throat red on the lower side, sweetly scented and opening in the mid to late afternoon; *perianth tube* cylindric, slightly expanded in the upper 5 mm, 25–34(–40) mm long, usually inclined; *tepals* subspathulate, widest in the upper third, ± clawed (rarely with a toothlike callus on each of the 3 lower tepals), the margins undulate, nearly equal in size or the uppermost often slightly larger, 9–12(–15) mm long, 3–4 mm wide, the lower 3 closer together, forming a lip, the uppermost often slightly larger than the others and held apart, ± upright to reflexed at right angles to the tube. *Filaments* unilateral, exserted for 3.5–5 mm, white; *anthers* parallel and contiguous, 4.5–6 mm long, light purple; pollen cream. *Ovary* ca.

2 mm long, ovoid; *style* arching over the stamens, dividing between the middle and apex of the anthers or sometimes exceeding them, branches spreading, virtually undivided or notched apically, ca. 2 mm long. *Capsules* obovoid to globose, 5–6 mm long; *seeds* globose, ca. 2 mm diam. *Chromosome number* $2n = 10, 6$.

Flowering time. January to April, rarely late November or December.

Distribution and habitat. A relatively common species of the dry interior plains of southern Africa, *Lapeirousia bainesii* extends from near Windhoek in central Namibia to the Cunene River in the north, into southern Angola, and across the Kalahari to eastern Botswana and the northwestern Transvaal (Fig. 14). It favors hard flat sandy ground where the corms may be lodged up to 30 cm below the surface. I have never seen it in rocky terrain, where it apparently is replaced by the related and morphologically similar *L. otaviensis*. The flowers open in the late afternoon and last through the night and into the following day, then they wilt rapidly in the dry, hot daylight conditions. The freshly opened flowers have a strong sweet and pleasant fragrance and produce abundant nectar. *Lapeirousia bainesii* is probably pollinated by hawkmoths. Like several other species of *Lapeirousia* in Namibia (see Ethnobotany), the corms of *L. bainesii* are reportedly eaten raw or roasted by the native population (Rodin, 1985).

Diagnosis and relationships. A long perianth tube, whitish perianth with pink to red markings near the base of the lower tepals, and a divaricately branched inflorescence with the branches bearing one or rarely two flowers immediately distinguish *Lapeirousia bainesii*. The perianth tube is usually (< 20)25–35(–40) mm long. The corm tunics are composed of light brown, densely compacted fibers, the outer layers of which become increasingly reticulate with age. These corm tunics, combined with the pale, long-tubed flower and a basic chromosome number of $x = 5$, suggest a close relationship with *L. otaviensis* and *L. schimperi*, and to a lesser extent with *L. gracilis*, which has a different karyotype (Goldblatt, 1990b) but also $n = 5$. The similarity in the size and general shape of the flowers of *L. otaviensis*, *L. gracilis*, and *L. bainesii* has led to much confusion in the past, but field studies in Namibia have indicated convincingly that these are three separate species with different ranges and habitat preferences as well as slightly different flowers and inflorescence structures (Figs. 12–14).

Specimens from central Botswana near Macheng, *Hansen 3357*, appear to represent a very odd form of *L. bainesii*. The flowers have a short tube 14–20 mm long (vs. 25–35 mm long in most other collections of the species). In other respects the plants accord with *L. bainesii*, including the fairly distinctive perianth coloring. The collection may represent a hybrid population, then most likely with *L. sandersonii*, the only other species of *Lapeirousia* recorded from this part of Botswana.

One of the few collections that I have seen from Angola, *Barbosa & Moreno 10181* from Chibia, is unusual in having a wine red perianth tube. The reverse of the outer tepals is a similar dark color, although the condition in the living plants may have been somewhat different. The significance of this variation cannot be properly assessed until more material from Angola can be examined.

History. Apparently first collected in 1863 by the nineteenth-century English landscape artist Thomas Baines and named in his honor, *Lapeirousia bainesii* was described by J. G. Baker in 1876. The species was based largely on Baines's collection but also on a second gathering from the Transvaal made by a certain Mr. Todd, about whom I have not been able to obtain information. Baines's plants were collected in western Botswana near Kobe Pan, an area still poorly known botanically.

Plants from west central Namibia were described in 1922 as the separate *Lapeirousia vaupeliana* by Dinter, based on three of his own collections. The distinction that Dinter made between this and the avowedly related *L. bainesii* was the red-violet flower with darker veins in his species compared with the white flowers of *L. bainesii* with dark brown markings. These differences do not seem significant and certainly do not merit recognition of *L. vaupeliana* as a separate species.

Lapeirousia otaviensis was regarded as a synonym of *L. bainesii* by Sölch (1969) in his treatment for the *Prodromus Flora von Südwestafrika*. However, he upheld *L. vaupeliana*, distinguishing it in the diagnostic key by the ultimate branches of the inflorescences each bearing a single flower in contrast to *L. bainesii*, in which the ultimate branches are spikes (i.e., with two or more sessile flowers). In fact the type specimen of *L. bainesii* has single flowers on the ultimate inflorescence branches and is conspecific with the later *L. vaupeliana*, whereas *L. otaviensis*, with its 3–5-flowered inflorescence branches and different flowers, is distinct from *L. bainesii*.

Additional specimens examined. ANGOLA. HUILA: 16

km from Quihita to Vila de Joâo de Almeida (Chibia), black soil under *Acacia*, *Barbosa & Moreno 10181* (COI, LISC). CUNENE: Namakunde, *Barnard 139* (SAM); *Rautanen 702* (Z). BOTSWANA. NGAMILAND: 19.21 (Aha Hills) Aha Hills, 110 km W of Nokaneng (CB), *Wild & Drummond 6919* (BM); Dobe, 26 km N of Aha Hills, SWA border (CA), *Wild & Drummond 7202* (K, PRE); 20.21 (Koanaka Hills) near SWA border fence, sandy grassland, (?), *Smith 3330* (MO); 20.23 (Kwebe Hills) Ngamiland, Kwebe, *Lugard 179* (GRA, K). CENTRAL: 20.25 (Mompse) Odiakwe, savanna, W of Francistown just N of Mkarikari Pan (AB), *Wild & Drummond 6826* (K); 21.25 (Lothlekane) Ngamiland, near Bachakuru, white and chocolate (DD), *Lugard 242* (K); 23.26 (Mahalapye) Mahalapye Exp. Morale, shallow gritty sandy loam (BB), *Yalala 356* (K, LISC, PRE); Mahalapye, *Camerik 215* (PRE); 23.27 (Ellisras) 10 mi. W of Macheng towards Mahalapye, woodland, 23°10″ 27°20″ (AB), *Hansen 3357* (C, K, PRE, WAG). KGATLENG: 24.26 (Mochudi) Mochudi (AC), *Harbor* sub *Rogers 6569* (G, K, PRE); *Harbor s.n.* (PRE 14060). NAMIBIA. ETOSHA: 18.14 (Otjitundua) Etosha National Park, S of Okawao, red chalky sand (DD), *Giess & Loutit 14195* (WIND); 19.14 (Kamanjab) Etosha National Park, Kaross (B), *Volk & Le Roux 808* (PRE, WIND). OKAVANGO: 17.19 (Rundu), 14.6 mi. E of Runtu on Sambiu road (DD), *de Winter & Marais 4558* (K, M, WIND); 17.20 (Sambio) Masari, Kavango (CC), *Vorster 2788* (PRE); 18.19 (Karakuwise) Cigarette, NE of Karakuwise (DC), *Maguire 2217* (NBG), *2381* (NBG, PRE); 19.20 (Tsumkwe) 300 m S of main Tsumkwe–Grootfontein road, border of Agriculture Dept. farm (CB), *Hines 363* (WIND); 6 km E of Tsumkwe on the road to Botswana, white sand (DA), *Giess et al. 11033A* (WIND). OVAMBOLAND: 17.15 (Ondangua) Odanga, no date (DD), *Barnard 195* (SAM), *199* (SAM); 100 km E Oshikango, corm eaten raw or roasted (BD), *Rodin 9295* (K, M, MO, PRE, WIND). KAPRIVI: 18.21 (Andara) Bagani Camp, Kaprivi side of river (BA), *de Winter & Wiss* (PRE). GROOTFONTEIN: 19.16 (Gobaub) farm Norabis 387, W of Otavi, thornveld on red sandy loam (DD), *Goldblatt & Manning 8826* (MO, PRE, WIND); 19.17 (Tsumeb) Otavi (CB), *Dinter 5755* (B, G, PRE, Z); Grootfontein, Otjirukaku (DB), *Seydel 2068* (B, BR, C, GH, K, M, MO, S, WAG, WIND); 19.18 (Grootfontein) farm Oliewenhof, sehr häufig auf der Palmflache (CB), *Merxmüller & Giess 30153* (K, M, WIND, PRE, S, SRGH, WAG); 20.16 (Otjiwarongo) farm Wittenberg 90, red sand, *Goldblatt & Manning 8832* (MO). OKAHANDJA: 21.16 (Okahandja) Omatako View (BA), *Woortman 152* (M, WIND); 20.17 (Waterberg) Quickborn, sand (AA), *Bradfield 196* (K, PRE). OUTJO: 20.16 (Otjiwarongo) Outjo (AA), *Rautanen 389* (Z). WINDHOEK: 21.17 (Otjosondu) 48 km along Kapps Farm road from Steinhausen, compact sand (DC), *Goldblatt & Manning 8808* (E, K, M, MO, NBG, PRE, S, WAG, WIND). GOBABIS: 21.18 (Steinhausen) deep red sand, farm Mex, pink to white, (AB), *Immelman 526* (K, PRE); farm Mex, 45 km N of Witvlei, red sand, *Germishuizen 2662* (PRE, WIND); 21.19 (Epikuro) Epikuro Reserve 30 mi. NE of Epata, Eiseb Omuramba (AA), *Giess 9746* (WIND); 23.18 (Leonardville) sandfeld, Gamoros (cult.) (AB), *Dinter 2788a* (SAM). KEETMANSHOOP: 25.18 (Tses) Kalaharirand, Tutara, farm Okamatangara (DB), *Seydel 2549* (BR, K, M, MO, SRGH, WAG). SOUTH AFRICA. TRANSVAAL: 22.29 (Waterpoort) Dongola Reserve, 10 mi. SE Reserve, farm Coila (AD), *Codd & Dyer 3780* (E, K, PRE); Dongola, Zoutpansberg (BC), *Pole Evans 4305* (K, MO, PRE, SRGH); Soutpansberg, 1.5 mi. NW of Wyliespoort, 2,800 ft., *Codd 8367* (PRE); 23.27 (Ellisras) Potgietersrust District, 2 m NE Tomburke, red gritty flats (BB), *Codd 6614* (K, PRE, SRGH); 19 mi. E of Ellisras, cultivated land (DB), *Louw 3506* (AAU). WITHOUT PRECISE LOCALITY: BOTSWANA: Bakwena Territory, Sirorume River S of Tropic of Capricorn, *Holub s.n.* (K).

14. Lapeirousia schimperi (Aschers. & Klatt) Milne-Redhead, Kew Bull. 307. 1934. Quezel, Fl. Veg. Pl. Darfur & Jeb Gourgeil (Dossiers Rech. Coop. Prog. 45: 134. 1969. Cufodontis, Enum. Pl. Ethiopiae Sperm. 2: 1592. 1972. Wickens, For. Bull. new ser. 14: 39. 1969; Fl. Jebel Marra 158. 1976. *Tritonia schimperi* Aschers. & Klatt, Linnaea 34: 697. 1866. Schweinfurth, Beitrag Fl. Aeth. 1867. [*Acidanthera unicolor* Hochst. ex Baker, J. Linn. Soc. Bot. 16: 160. 1878; Handbk. Irideae 188–189. 1892; Fl. Trop. Africa 7: 359. 1898, nom. superfl. pro *Tritonia schimperi* Aschers. & Klatt (1866) (Schimper, Plantae Abyssinicae 2304).] TYPE: Ethiopia. Tigray: woods and thickets near Goelleb on the river Tacazze, 4,000 ft., *Schimper 2304* (lectotype, B, here designated; isolectotypes, K, P); Yemen: *Schimper s.n.* (syntype, B?, not seen and perhaps lost). Figure 15.

Lapeirousia angolensis (Baker) R. Foster, Contr. Gray Herb. 114: 48. 1936. *Anomatheca angolensis* Baker, J. Bot. 14: 337. 1876. [*Lapeirousia monteiroi* Baker, Fl. Trop. Africa 7: 355. 1898, nom. illeg. superfl. pro *A. angolensis* Baker.] TYPE: Angola. Without precise locality, cult. Kew, *Monteiro s.n.* (holotype, K).

Lapeirousia fragrans Welw. ex Baker, Trans. Linn. Soc. London (Bot.) ser. 2, 1: 272–273. 1878. TYPE: Angola. Huila: ad Morro de Lopollo, 5,200 ft., stony and rocky places, Dec. 1859, *Welwitsch 1552* (holotype, K; isotypes, BM, C, COI, G, P).

Lapeirousia cyanescens Welw. ex Baker, Trans. Linn. Soc. London (Bot.) ser. 2, 1: 272. 1878. Sölch, Prod. Fl. Südwestafrika 155: 9. 1969. Cufodontis, Enum. Pl. Ethiopiae Sperm. 2: 1592. 1972. TYPE: Angola. Huila: hills near Humpata, Apr. 1860, *Welwitsch 1553* (lectotype, K, here designated; isolectotypes, B, BM, COI, G).

Lapeirousia edulis Schinz, Bull. Herb. Boissier 4 (Appendix 3): 49. 1896. TYPE: Namibia: Amboland, W of Olukonda, 5 Apr. 1893, *Rautanen 106* (lectotype, Z, here designated; isolectotypes, K, P (2), Z (3)).

Lapeirousia porphyrosiphon Baker, Fl. Trop. Africa 7: 353. 1898. TYPE: Botswana. Ngamiland: Kalahari Desert near Mamunwe, 26 Feb. 1897, *Lugard 338* (holotype, K).

Lapeirousia erythreae Chiovenda, Ann. Bot. Roma 9: 139. 1911. TYPE: Ethiopia. Eritrea: Acchelé Guzai (Ocule Cusai) near Loggo Sarda, Deggahen, 2,600 m, 15 Sep. 1902, *Pappi 1414* (lectotype, G, here designated; isolectotypes, GH, MO); Bogos near

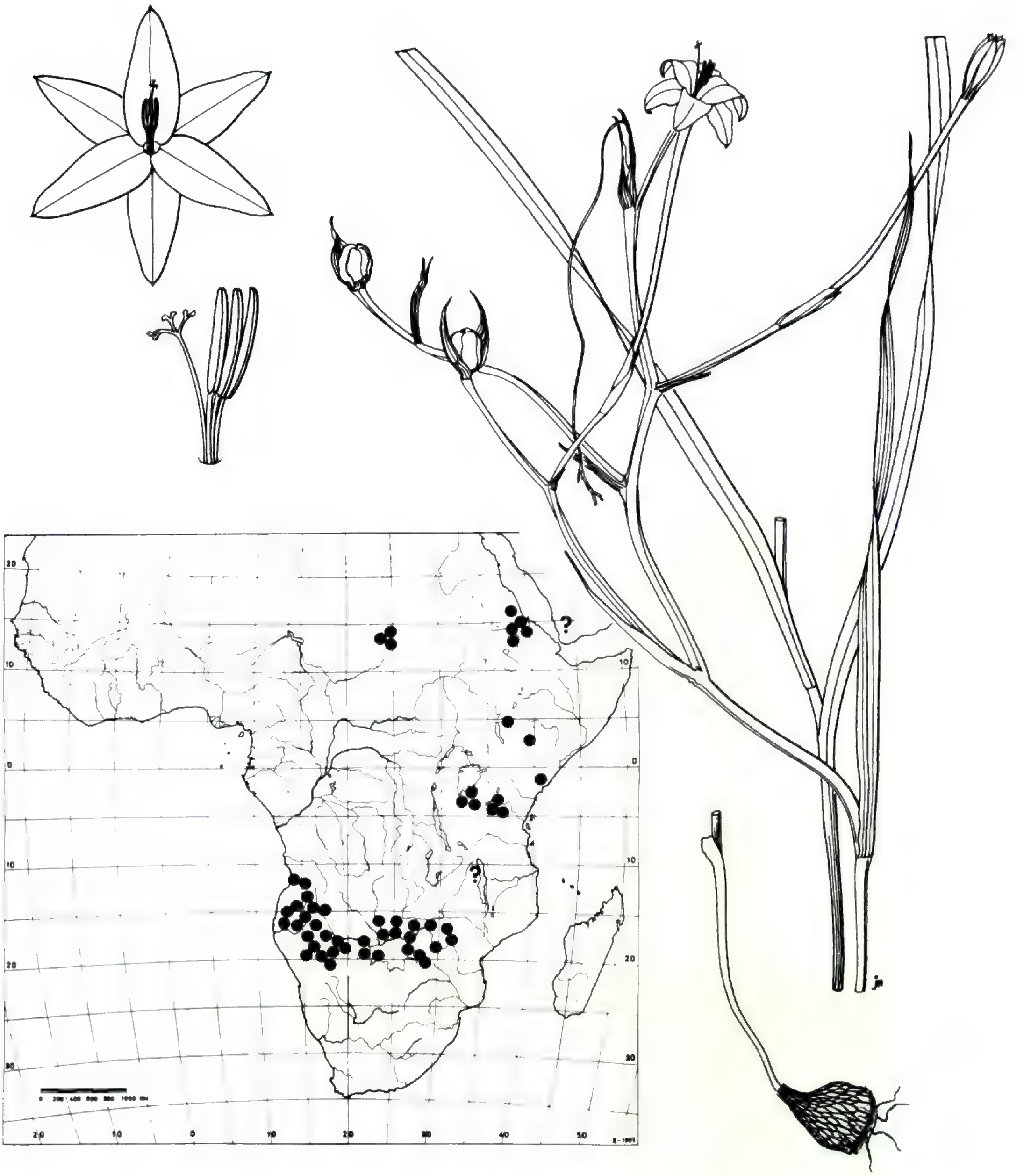

FIGURE 15. Morphology and distribution of *Lapeirousia schimperi*. Stations in Malawi and Yemen indicated with a ? require verification and remain doubtful. Habit and corm × 0.5; single flower full size; details of stamens and style × 2.5. (Drawn by J. C. Manning.)

Cheren, 24 Aug. 1903, *Pappi 7088* (? FI, not seen); Dembelas towards the Mai Albo, 25 Sep. 1903, *Pappi 6072* (? FI, not seen).

Lapeirousia montaboniana Chiovenda, Ann. Bot. Roma 9: 140. 1911. TYPE: Ethiopia. Eritrea: Bogos near Cheren, 24 Aug. 1906, *Pappi 7087* (? FI, not seen).

Lapeirousia uliginosa Dinter, Die vegetabilische Veldkost Deutsch-Südwest-Afrikas 13–14. 1912. TYPE: none cited.

Lapeirousia dinteri Vaupel, Bot. Jahrb. Syst. 48: 544–545. 1912. TYPE: Namibia: Damaraland, Aukos-Kreyfontein, 28 Dec. 1908, *Dinter 810* (holotype, B; isotypes, B, SAM (2)).

Plants (20–)30–80 cm high, usually several-branched. *Corm* 18–22 mm diam. at the base, tunics composed of compacted fibers, light to dark brown, the outer layers becoming loosely fibrous and reticulate. *Leaves* linear, 3 or more, the lower 2 largest and usually slightly longer than the inflorescence, decreasing in size above and becoming bractlike, narrowly lanceolate, 5–10(–15) mm wide,

the midrib lightly raised. *Stem* rounded below, to nearly square and 4-angled to 4-winged above. *Inflorescence* a lax pseudopanicle, the ultimate branches with 1–3 sessile flowers; *bracts* ± equal, (10–)20–35(–45) mm long, herbaceous becoming membranous above to almost completely dry and papery, then light to dark brown, apices dark brown. *Flowers* zygomorphic, white to cream, rarely pale violet, when whitish sometimes fading or drying lilac especially on the tube, opening in the evening and then sometimes scented; *perianth tube* cylindric, slender, 10–14(–15) cm long; *tepals* lanceolate, extended ± at right angles to the tube, 18–22 mm long, 6–7 mm at the widest. *Filaments* unilateral, erect, exserted 5–7 mm from the tube; *anthers* parallel and usually contiguous, 6–7 mm long, cream; pollen cream. *Ovary* ca. 4 mm long, rapidly elongating after fertilization; *style* filiform, arching behind the filaments, dividing at or up to 3 mm beyond the anther apices, branches ca. 2 mm long, forked for ca. ⅓ their length. *Capsules* obovoid-oblong, 8–12 mm long, partly enclosed in the bracts; *seeds* globose to slightly angular, sometimes tapering to a persistent funicle, 2–2.5 mm diam. *Chromosome number* $2n = 10$.

Flowering time. Mid to late summer, December to March, in central and south tropical Africa; north of the equator mostly in September and October, in Kenya and Ethiopia also April to June.

Distribution and habitat. Lapeirousia schimperi has a remarkably wide distribution across Africa (Fig. 15). It extends from southwestern Angola, north-central Namibia, and northern Botswana through southern Zambia to Zimbabwe in an almost continuous belt. Further north its distribution is scattered, and it occurs in northern Tanzania, eastern Kenya, southern Ethiopia, disjunctly in northern Ethiopia, and the Jebel Marra and Jebel Gurgeil highlands of northwest Sudan. It is almost certainly absent from Zaire, Uganda, central and western Kenya, and southern Tanzania, but the species probably occurs in western Somalia (although I have seen no records from there). A plant from Yemen is cited in the protologue, but I have seen no collections from this country. I have also had seeds of plants said to have been collected on the Nyika Plateau in Malawi. The Malawi and Yemen records require confirmation. Despite the questions about the distribution of *L. schimperi*, there is no doubt that it is absent from large parts of tropical Africa, and its unusual discontinuous range is noteworthy.

Lapeirousia schimperi grows in moist situations in otherwise largely arid country. It typically occurs in washes, the so-called omurambas of Namibia, dambo margins, stream sides, seasonal marshes, and in damp grassland. The flowers open in late afternoon and last through the night, but gradually wilt the next day. Some collections note a sweet fragrance when the flowers are open, but live plants from Namibia that I have examined were scentless, suggesting variation in this character. The edible corms are eaten either raw or roasted by the Ovambo of northern Namibia (Rodin, 1985) and the Kung Bushmen (Marshall, 1976).

Diagnosis and relationships. The large white flower with a perianth tube 10–15 cm long and the laxly branched inflorescence distinguish *Lapeirousia schimperi* readily from most other species in the genus. The paniculate inflorescence, plane leaves with a well-defined midrib, and corm tunics of compacted fibers place it in sect. *Paniculata*. It has no obviously close relatives in this alliance, composed largely of plants with small flowers and typically multibranched pseudopanicles with crowded flowers. Its basic chromosome number, $n = 5$, and karyotype (Goldblatt, 1990b) and usually light brown, fairly fibrous corm tunics are shared with *L. otaviensis* and *L. bainesii*, suggesting that they may be the closest allies of *L. schimperi*. Those two species, centered in northern Namibia and adjacent Botswana, also have pale flowers with relatively long perianth tubes, but their inflorescences are more compact, and they are not likely to be confused with *L. schimperi*.

Unusually long-tubed white flowers characterize two other tropical African species of *Lapeirousia*, *L. odoratissima* and *L. schinzii*, both of which have corrugate leaves and woody corm tunics, which place them in sect. *Lapeirousia*; the floral similarity must be due to convergence. Presumably all are pollinated by hawk moths.

Lapeirousia schimperi exhibits relatively little variation for a species with such a wide distribution. Some specimens from Angola and Namibia in the southwest of its range have unusually short bracts in the 15–20 mm range (e.g., *Giess & Loutit 14123*), but at least some plants from Namibia have bracts up to 35 mm long, thus comparable to those in plants from tropical and northeastern Africa in which the bracts range from 35 to 45 mm.

Some collections from Ethiopia and Sudan (e.g., *Schimper 2304, 431*) also have pale or fairly dark brown, particularly short bracts 10–15 mm long. Their flowers have a perianth tube 7–8 cm long. Such plants may be depauperate owing to a particularly dry growing season, or they may represent

an ecotype or race that constantly has these features.

History. Although a well-defined species, *Lapeirousia schimperi* has a long and confused history. This is largely due to its wide distribution rather than to any conviction that its synonyms were species distinct from those from distant parts of its range. The type locality is in northern Ethiopia, where collections were made in the 1840s by Quartin Dillon and Petit and later by Schimper in 1852–1864. The species was named in Schimper's honor by Ascherson & Klatt (1866), who referred it to the otherwise southern African genus *Tritonia*. Three separate collections from southwestern Angola made at this period by Joachim Monteiro and Friedrich Welwitsch were described by J. G. Baker as *Anomatheca angolensis* (1876), *L. cyanescens* (1878), and *L. fragrans* (1878), respectively, without reference to the Ethiopian species. Later collections from Namibia were named independently by Hans Schinz as *L. edulis* in 1896 and Friedrich Vaupel as *L. dinteri* in 1912. Plants from Botswana, collected by E. J. Lugard, were assigned to *L. porphyrosiphon* (Baker, 1898), while in 1911 A. Chiovenda described *L. erythreae* and *L. montaboniana* based on contemporary collections from Eritrea. Only in 1934 was *Tritonia schimperi* transferred to *Lapeirousia*, but for many years the name *L. porphyrosiphon* was used for the species in south tropical Africa.

Additional specimens examined. ANGOLA. CUANZO SUL: road from Nova Redondo to Lobito, 60 m, 17 Apr. 1969, *Teixeira et al. 11412* (LISC). CUNENE: Rocades, centro do Estudos do Cunene, *da Silva 2991* (BR, K, PRE); Humbe, bords du Cunene, Tyipelongo-Mucope-Donguena, s.d., *Bonnefoux & Villain 58* (P). HUAMBO: Cuima, Eleude Mission, Dec. 1940, *Faulkner A390* (K, PRE); road from Nova Lisboa to Luanda, Serra do Cussava, 26 Dec. 1970, *Moreno 311* (LISC, M); vicinity of Nova Lisboa near Cruzeiro, banks of Cuando River, 26 Mar. 1971, *da Silva 3522* (LISC, PRE); Chianga, ca. 1,700 m, 5 Mar. 1962, *Teixeira & Andrade 6542* (COI, LISC). HUILA: hills near Humpata, Feb. 1899, *Antunes 724* (P), Mar. 1902, *DeKindt 3213 (449)* (LISC, P); Tundavala, 14°50″ 13°22″, 2,230 m, 7 Mar. 1973, *Bamps et al. 4057* (BR, K, LISC); Quilengues–Chingoroi, 5 Dec. 1962, *de Menezes 384* (K, LISC, PRE, SRGH); Chitanda munding, 1,100 m, 28 May 1905, *Baum 949* (BM, COI, E, G, K, M, S, Z); Caconda, Mar. 1880, *Anchieta 15* (LISU); Mar. 1882, *Anchieta 34* (LISU); Dec. 1882, *Anchieta 131* (LISU); Ganguelas, Vila Artur de Paiva–Cutato, *Mendes 3329* (LISC); Vila Artur de Paiva (Vila de Ponte), granja da administracão, 1,470 m, 1 Jan. 1960, *Mendes 1919* (LISC); near Huila, *Mendes 1512* (LISC); Sá da Bandeira, *Torre 8629* (LISC). NAMIBE: hills on road between Namibe (Mossamedes) and St. Nicolau, *Kers 3646* (PRE). BOTSWANA. NGAMILAND: 17.25 (Livingstone) S side of Chobe River, above Kasane, May 1972, *Sheppe 167* (SRGH); 18.21 (Andara) SW end of Tsodilo Hills, open savanna, 11 Mar. 1985 (DD), *Long 12330* (E); 19.23 (Maun) Khwai/Maxwe road, Moremi Wildlife Reserve, 16 Mar. 1977 (BC), *Smith 1936* (BR, K, SRGH). ETHIOPIA. SIDAMO: near the Sagan River, ca. 500 m, 37°45″ 4°47″, *Acacia* woodland in grass, 27 May 1974, *Sandford* sub *Ash 2498* (K). TIGRAY: near Goelleb on River Tacazze, 4,000 ft., 28 Aug. 1854, '*A. unicolor*' *Schimper 2304* (BM, K, P). GONDER: Simen, Dsha Dsha, 22 Aug. 1853, *Schimper 431* (P). KENYA: Somali border, open grassland, 23 Aug. 1961, *Gillespie 250* (BR, K, P); Kiunga, 55 mi. NE of Lamu, 9 Aug. 1961, *Gillespie 176* (BR, K); Kaiunga, 5 Apr. 1910, *Battiscombe 231* (K); Dandu, eroded gravels at foot of mountain, 4 June 1952, *Gillett 13426* (K). NAMIBIA. OVAMBOLAND: 17.15 (Ondangua) 100 km E of Oshikango, 19 Apr. 1973 (BD), *Rodin 9295A* (M, MO, PRE, WIND). OKAVANGO: 17.18 (Kuring Kuru) Katui-Tui, maize land in sandy loam, 15 May 1965 (fr) (AD), *Barnard 191* (WIND); Kuring-Kuru, Okavango riverbank in forest, 28 Mar. 1966 (DA), *Soni s.n.* (WIND 3938); 17.19 (Runtu) swampy marshes below Runtu, 31 Jan. 1956 (AD), *de Winter & Marais 4469* (K, M, PRE, WIND, Z); 18.19 (Karakuwisa) grass flats, Karakuwisa, 4 Mar. 1958 (DC), *Merxmüller & Giess 1795* (BM, K, M, PRE, WIND); 18.21 (Andara) Kaprivi side of the river at Andara Mission, crevices on rocky outcrops, 23 Feb. 1956 (AB), *de Winter & Marais 4820* (K, PRE, WIND); Okavango River, 19 km N of Shakawe on the Botswana border, 16 Mar. 1965 (BA), *Wild & Drummond 7093* (K, LISC, M, PRE, SRGH). KAPRIVI: 17.24 (Katima Mulilo) Katima Mulilo, vlei, 30 Jan. 1975 (AD), *Vahrmeijer & du Preez 2496* (MO, PRE). ETOSHA: 18.16 (Namutoni) Etosha National Park, Bigales Huh, 15 Feb. 1974 (C), *Le Roux 644* (PRE, WIND); 19.15 (Okakuejo) Etosha Pan, black peat soil on the road to Ombika, 4 Apr. 1980 (BB), *Giess 15472* (M, MO, PRE, WIND); Etosha National Park, 2.5 km E of Okakuejo–Ombika road, 5 Mar. 1976 (BD), *Giess & Loutit 14123* (K, M, MO, PRE, WIND); gray-black peat flats N of Ombika, *Le Roux 321* (PRE, WIND); 19.16 (Gobaub) Etosha Game Park, near Homob water hole, 11 Feb. 1966 (AA), *Tinley 1285* (M, PRE, WIND). GROOTFONTEIN: 19.16 (Gobaub) farm Neidaus North 78, heavy black clay with limestone, seasonally waterlogged, 19 Mar. 1988 (DC), *Goldblatt & Manning 8831* (MO, WIND); 19.17 (Tsumeb) farm Malta, 5 Feb. 1971 (AB), *Giess 11226* (M, PRE, WIND); farm Kumkauas, large colonies among tough grasses, 30 Jan. 1971 (CA), *Giess 11212* (M, WAG, WIND); 9 Mar. 1974, *Merxmüller & Giess 30175* (K, M, PRE, S, SRGH, WAG, WIND). SUDAN. DARFUR: Jebel Marra, E of Zalinjea, 3,500 ft., poorly drained, 13 Aug. 1964, *Wickens 2101* (K); Suni–Tuora Tanje, 7,800 ft., moist soils, 21 Sep. 1964, *Wickens 2695* (K); Nyertete, 3,700 ft., *Wickens 2126* (K); Gur Lambang, lava soils, 6,300 ft., 17 Sep., *Wickens 2589* (K); 1 hour on path from Taurotonga to Kilokitting, 2,000 m, basalt, 15 Sep., *Jackson 4073* (K). TANZANIA. ARUSHA: Magugu/Sangaiwe Hills, 70 mi. WSW of Arusha, 3,500 ft., Mar. 1967, *Beesley 265* (BR, K); Mbulu District, Tarangire National Park, 1,066 m, 14 Feb. 1970, *Richards 25422* (K). DODOMA: Great North Road, Kalo, 15 mi. N of Kondoa, 5,050 ft., black clay in vlei, 11 Jan. 1962, *Polhill & Paulo 1132* (BR, K, LISC, P, PRE). MWANZA: Mwanza, s.d., *Davis 180* (K). SHINYANGA: near Shinyanga, Jan. 1933, *Bax 399* (BR, K); Huruhuru–Mantini road, Shinyanga, 3,800 ft., 16 Jan. 1932, *Burtt 3511* (BM, BR, K); Nindo, Jan. 1972, *Stefanescu 125* (K). ZAMBIA. SOUTHERN: Livingstone, 20 Jan. 1929,

Grant 4507 (MO, PRE); Victoria Falls road, Livingstone, 20 Jan. 1919, *Young 17315* (BM); Kafue basin, Monze near Lochinvar Ranch, mixed *Acacia* woodland, 31 Jan. 1964, *van Rensburg KBS2708* (K, SRGH). WESTERN: Machili, dambo margin, *Fanshawe 6243* (NDO, SRGH); Machili basin, *Martin 725* (BM, NDO); Masese, pan margins, 9 Jan. 1961, *Fanshawe 6098* (BR, K, NDO, SRGH). ZIMBABWE. MASHONALAND CENTRAL: N of Sipolilo, 30 Jan. 1948, *Whellan 313* (K, LISC). MASHONALAND EAST: near Salisbury, *Young* sub *Moss 17315* (K). MASHONALAND WEST: Urungwe District, Mense Pan, 11 mi. ESE of Chirundu bridge, *Drummond 5346* (BM, BR, K, LISC, PRE, SRGH). MATABELELAND NORTH: Bulawayo, Feb. 1923, *Borle 361* (K, M, PRE); 7 Jan. 1898, *Rand 232* (BM); Victoria Falls, Jan. 1905, *Allen 146* (K, SRGH); Jan. 1906, *256* (K, SRGH); Jan. 1910, *Rogers 5415* (K, SRGH, WAG, Z); Wankie National Park, Sinamatella Dam ca. 1 mi. from the camp, 24 Feb. 1967, *Rushworth 174* (MO, SRGH); Wankie, Shapi Camp, Kalahari sand, 27 Feb. 1967, *Rushworth 269* (BR, K, LISC, PRE, SRGH); Wankie, Shapi road, in vlei, 15 Feb. 1956, *Wild 4747* (K, PRE, SRGH); Insiza District, Shangani, farm Bon Accord, cracks in granite whalebacks and in black vlei soil, 26 Jan. 1976, *Glasse s.n.* (C, MO, SRGH); Nyamandhlovu, Pasture Station, black vlei soil, *Plowes 1661* (K, LISC). MATABELELAND SOUTH: Matobo District, 3 Feb. 1948, *West 2678* (MO, SRGH); 7.2 km S of Bulawayo Post Office, S side of Johannesburg road, *Acacia* woodland, 22 Jan. 1976, *Cross 340* (K, MO, PRE, SRGH). MIDLANDS: Que Que to Gwelo, main road, *Davey 1* (K, PRE, SRGH). WITHOUT PRECISE LOCALITY: ?ANGOLA: 1878, *Capello 20* (LISU); *Welwitsch 4108* (P). BOTSWANA: Ngamiland, Jan. 1931, *Curson 75* (PRE). ETHIOPIA: Tigre & Begemdir, 21 Aug. 1862, *Schimper 909* (BM); Habab, 5,000 ft., Sep. 1872, *Hildebrandt 374* (BM); Abba Heruke, 6 Aug. 1852, *Schimper s.n.* or *431* (P); Masser, 4 Sep. 1853 (fr), *Schimper s.n.* or *431* (P). NAMIBIA: Kapichu, Mar. 1923, *Barnard 137* (SAM).

SUBGENUS *LAPEIROUSIA* SECTION *SOPHRONIA*
(LICHT. EX ROEMER & SCHULTES)
GOLDBL. & MANNING

15. Lapeirousia littoralis Baker, Trans. Linn. Soc. London, Bot. ser. 2, 1: 273. 1878. TYPE: Angola. Namibe: sandy coastal hills ad Praia da Amelia prope Villa de Mossamedes, July 1859, *Welwitsch 1546* (holotype, BM—see discussion of the type specimen).

Synonyms are listed under the two subspecies.

Plants (5–)10–35 cm high, simple or often with 1–few(or many) branches, these either long or clustered near the base. *Corm* campanulate, 10–14 mm wide at the base, tunics woody, brown, the outer layers breaking irregularly, rarely becoming fibrous, the basal margin crennate or rarely bluntly denticulate. *Cataphylls* usually 2, the outer one short and the inner reaching almost to ground level, membranous. *Leaves* few to several, linear, 1.5–4 mm wide, lightly corrugate, the lowermost inserted at or just below the ground and longest, often as long as the inflorescence or rarely somewhat longer, ascending to falcate or trailing, upper leaves progressively shorter. *Stem* simple or branched, the branches either crowded below or laxly arranged, ± rounded to weakly angled below the nodes. *Inflorescence* comprising 1–several lax to fairly congested branches of 5–12 flowers; *bracts* herbaceous, weakly keeled, the outer 10–20(–25) mm long, the inner smaller, becoming membranous, apically forked. *Flowers* zygomorphic, white to cream, greenish yellow, or light purplish brown, with a strong sweet fragrance; *perianth tube* ± dimorphic, slender below, curving outward and expanded above, (20–)30–45(–70) mm long, the upper part ca. 6 mm long; *tepals* subequal, narrowly lanceolate to linear-filiform, 13–30 mm long, 1.3–2.5(–3) mm wide, acute to attenuate, spreading equally at right angles to the tube, vertical. *Filaments* unilateral and arcuate, exserted 2–3 mm; *anthers* parallel, 4–5 mm long, cream; pollen cream. *Ovary* globose, ca. 3 mm long; style arching behind the stamens, branching between the base and middle of the anthers, the branches divided for about ⅓ their length, ascending below, recurved above and usually tangled in the anthers. *Capsules* globose, 6–8(–11) mm long; *seeds* globose, ca. 2 mm diam. *Chromosome number* $2n = 16$.

Flowering time. Usually late December to March in tropical Africa (subsp. *caudata* and subsp. *littoralis*); September and October in southern Namibia and South Africa (subsp. *littoralis*) but also at other times.

Distribution and habitat. Lapeirousia littoralis occurs in a wide swath across south tropical Africa (southwestern Angola, northern Namibia, Zambia, Zimbabwe, Botswana, southern Mozambique) with southward extensions into the arid parts of southern and western Namibia and the northern Cape and Namaqualand in South Africa (Fig. 16). It blooms in the wet season, usually not long after the first soaking rains. Thus the Namaqualand and southern Namibian populations usually flower in the spring (August to October) following the winter rainfall that prevails along the southwestern African coast. Elsewhere populations generally flower in early to late summer, not long after the beginning of the summer rains of tropical and eastern southern Africa. In southern Mozambique populations appear to bloom in almost any month, reflecting the nonseasonal rainfall pattern of the southeast coast. *Lapeirousia littoralis* favors sandy, well-drained soils, sometimes occurring on sand dunes. The probable pollinators are moths, given the pale-

colored, very fragrant, long-tubed flowers. However, the style branches are tangled with the anthers, and self-pollination seems probable in the absence of insect-mediated pollen transfer.

Diagnosis and relationships. Characterized by pale, uniformly colored flowers with a long, dimorphic perianth tube that curves outward and is expanded above, *Lapeirousia littoralis* can usually be recognized by its flowers alone. Its vegetative and floral morphology are remarkably variable. Plants from northern Namibia, Zambia, Zimbabwe, and Mozambique have relatively long, sometimes lax spikes with short bracts 10–18 (–23) mm long and are usually 20–30 cm tall. The flowers in all collections from these relatively well-watered areas have long, narrow tepals 25–30 mm long and about 1.3 mm wide. As the flowers fade and dry, the tepals become distinctively filiform.

Plants from arid southwestern Angola, western and southern Namibia, and from the northwestern Cape and Namaqualand in South Africa tend to be shorter, often having the branches crowded at the base. In these plants the spikes are shorter, usually 10–15 cm high, and sometimes congested, and the bracts are usually 15–20(–25) mm long. The flowers in these populations have tepals about 20 mm long and 2–2.5 mm wide. When dry they do not always assume the filiform shape of the northern populations.

These two series of populations are usually easy to separate and might be regarded as different species except for the morphologically intermediate populations in central Namibia and southern Botswana that are often not easily assigned to either major group. The intermediates suggest that separation at subspecific rank is the most appropriate treatment for the southern and tropical populations of the species. The shorter form, first described by J. G. Baker in 1878 as *L. littoralis*, later as *L. burchellii* (1892), and then by Dinter as *L. ramosissima*, was first regarded as a subspecies of *L. caudata* by Goldblatt and Marais (Goldblatt, 1972), essentially for the reasons outlined above. *Lapeirousia streyi* from the Namib Desert south of the Kuiseb is regarded as belonging here, but it is close to being intermediate between the shorter subsp. *littoralis* and the taller subsp. *caudata*.

Plants from southern Mozambique, mostly from immediately around Maputo (Lourenço Marques), seem best treated as belonging to subsp. *caudata*. They stand out in having particularly long-tubed flowers and in often being very robust. The tubes are sometimes up to 7 cm long, compared with the 3.5–4 cm usual in central African plants. Floral

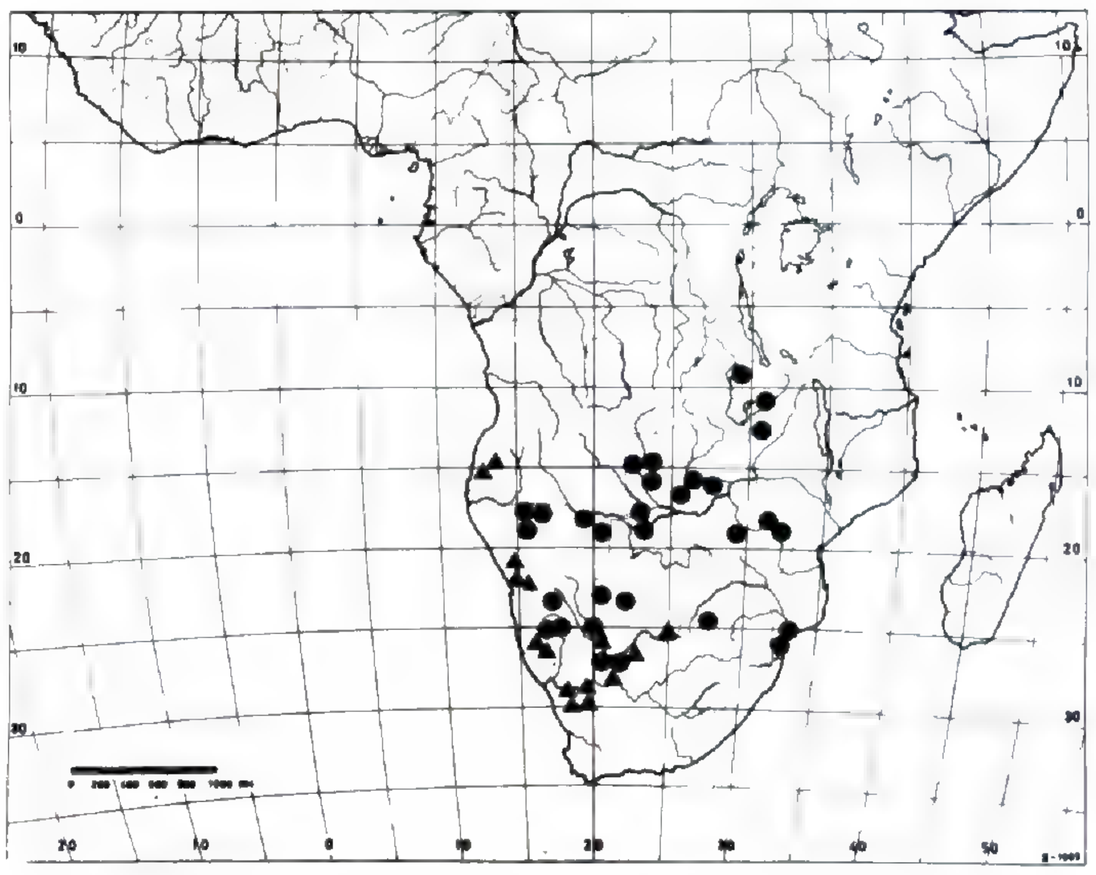

FIGURE 16. Distribution of *Lapeirousia littoralis*: subsp. *littoralis* represented by triangles, subsp. *caudata* by dots.

variation is notable also in plants from western Zambia, and a collection from Mongu (*Robinson 6749*) has flowers with perianth tubes 8–13 mm long and tepals ca. 18 mm long. Such isolated variation, particularly in tube length, also occurs in other species of *Lapeirousia* and appears to have no taxonomic significance.

Lapeirousia littoralis has a diploid number of $2n = 16$ and a dimorphic karyotype of one very long and seven short chromosome pairs. This is characteristic of subg. *Lapeirousia*, a largely western Cape and Namaqualand alliance comprising 17 species (Goldblatt, 1972) with corrugate leaves, woody corm tunics, and spicate or tufted inflorescences. There seems no doubt that *L. littoralis* belongs in this section despite its predominantly tropical distribution. The tufted tropical species, *L. odoratissima*, which has a larger flower with a perianth tube 10–14 cm long, seems most likely the closest relative of *L. littoralis*, an assumption based largely on the similarity of the flowers of the two species. Other species of sect. *Lapeirousia* that seem morphologically close to *L. littoralis* include the South African *L. arenicola* and *L. anceps*, both of which have long-tubed flowers with narrow tepals. In these two species the perianth has contrasting markings on the lower tepals unlike *L. littoralis*.

History. The fruiting type collection of *Lapeirousia littoralis* was made by Friedrich Welwitsch in July 1859, and was described by J. G. Baker in 1878, based solely on this collection. The type locality is near Mossamedes on gravelly hills around Praia da Amelia in southwestern Angola, now the province of Namibe. The type material is in poor condition and consists of depauperate plants with

branches produced from near the ground, bracts ca. 12 mm long, capsules ca. 9 mm long, and linear, lightly corrugate leaves. Alone the specimen cannot be matched with confidence, and until now *L. littoralis* has not been identified with any known species of the genus. However, another collection from southwestern Angola, *Torre 8824*, previously assigned to *L. caudata*, comprises plants that are clearly the same as those collected by Welwitsch, and they have flowers that correspond to the southern African and Namibian *L. caudata* subsp. *burchellii* (Goldblatt, 1972).

The latter taxon, based on *Lapeirousia burchellii*, was first recorded in October 1812 when the English botanist and explorer William Burchell reached the northern Cape. Burchell's collections were described formally by J. G. Baker in 1892 and were not considered to be a subspecies of *L. caudata*, the name used until now for *L. littoralis*, until later (Goldblatt, 1972). *Lapeirousia ramosissima*, collected near Gründorn in southern Namibia by Dinter and described by him, matches closely the type collections of *L. burchellii* and *L. littoralis*. A third species, *L. streyi* from west-central Namibia, is close to being intermediate between *L. littoralis* and plants from tropical Africa that have somewhat longer and narrower tepals and taller stems. These characteristics correspond to *L. caudata*, which was based on plants collected at Olukonda in northern Namibia and described by Hans Schinz in 1890. Plants matching *L. caudata* are now known to occur widely across south-central Africa from northern interior Namibia, across Zambia to Zimbabwe, with an isolated series of populations in southern Mozambique. Currently regarded as *L. caudata* subsp. *caudata* (Goldblatt, 1972), it now becomes *L. littoralis* subsp. *caudata*. The history of this subspecies is discussed below.

KEY TO THE SUBSPECIES OF *LAPEIROUSIA LITTORALIS*

1a. Perianth tube 28–35 mm long; tepals 13–15 mm long and 2–3 mm wide; bracts 15–20 (–25) mm long ..... 15b. subsp. *littoralis*
1b. Perianth tube (25–)30–45(–70) mm long; tepals 18–30 mm long and 1.3–2 mm wide; bracts 10–18(–23) mm long ..... 15a. subsp. *caudata*

15a. Subsp. caudata (Schinz) Goldbl., comb. et stat. nov. *Lapeirousia caudata* Schinz, Verh. Bot. Vereins. Brandenburg 31: 213. 1890. Baker, Handbk. Irideae 172. 1892. Sölch, Prod. Fl. Südwestafrika 155: 10. 1969. Goldblatt, Contrib. Bolus Herb. 4: 30–33. 1972. TYPE: Namibia: Amboland, Olukonda, *Rautanen 2* (lectotype, Z, designated by Sölch on the sheet; isolectotype, Z); Olukonda, *Schinz 2*, *15*, or *s.n.* (probable syntypes, G, K, Z).

Lapeirousia delagoensis Baker, Handbk. Irideae 171–172. 1892; Fl. Cap. 6: 94. 1896. TYPE: Mozambique: Delagoa Bay, Lourenço Marques, sandy places, *H. Bolus 7618* (lectotype, K, here designated; isolectotypes, BOL, G, SAM).

Lapeirousia lacinulata Vaupel, Bot. Jahrb. Syst. 48. 546–547. 1912. TYPE: Zambia: Kantanina Hills, *Kässner 2170* (holotype, B; isotypes, BM, BR, E, HBG, K, P, Z).

Plants 20–30 cm high, usually with a few long branches produced from near the base. *Inflorescence* a spike of 8–12 flowers; *bracts* 10–18(–23) mm long. *Flowers* with a perianth tube (25–)30–45(–70) mm long; *tepals* (18–)25–30 mm long and 1.3–2 mm wide, usually ± filiform, especially when dry.

Distribution. Subspecies *caudata* has a wide range across south-central tropical Africa (Fig. 16). It extends from northern Namibia across western and southern Zambia to Zimbabwe. There is also a series of isolated populations in southern Mozambique.

History and typification. Subspecies *caudata* was first gathered in 1885 at the Finnish Mission Station at Olukonda in northern Namibia by the Swiss botanist Hans Schinz. Schinz later described it in 1890 based on his and the Finnish missionary Martti Rautanen's ample but confusingly labeled collections at the Zurich Herbarium. A sheet collected by *Rautanen* in 1887 was designated the lectotype by Sölch in 1959 and this choice appears to be suitable.

Corresponding closely with *Lapeirousia caudata*, although from northern Zambia, *L. lacinulata* was collected by T. Kässner in 1906 and described by Vaupel in 1912. He distinguished *L. lacinulata* on the basis of its slender habit, low stature, and shorter perianth tube only 2.5 cm long (actually 2.5–2.8 cm), in contrast to *L. caudata* in which the perianth tube is 3–4(–7) cm long. The distinction seems minor and is not sufficient for the separation of the species. A few other collections of subsp. *caudata* have a similar short perianth tube but not the slender habit. The isolated Mozambican populations near Maputo were discovered by the missionary Henri Junod in 1890 and subsequently by the Cape botanist Harry Bolus in 1886. Bolus's collection was referred by J. G. Baker (1892) to the new species *L. delagoensis*.

Additional specimens examined. BOTSWANA. NGAMILAND: 18.23 (Siambiso) sandy floodplain of Kwando River, 18°5″ 23°20″ (AB), *Smith 2222* (K, PRE, SRGH).

KGALAGADI: 23.20 (Ukwi) 120 km WNW of Hukuntsi on track to Ncojane, 23°41″ 20°47″, open sandy savanna (DC), 13 Mar. 1979, *Skarpe 333* (K, PRE, SRGH, UCBG); 23.22 (Kang) Kang, 320 km W of Gaborone, 3,500 ft. (DD), 20 Oct. 1975, *Mott 772* (SRGH, UCBG). MOZAMBIQUE. MAPUTO: Delagoa Bay, near Lourenço Marques, 30 Nov. 1897, *Schlechter 11540* (B, BR, G, P, PRE, SAM); *Rogers 22475* (K, PRE); 1890, *Junod 24* (G, Z); 1896, *Junod 486* (G, P, Z); Costa do Sol, sand dunes, 2 Mar. 1960, *Balsinhas 126* (B, BR, K, LMA, P, PRE); 22 July 1965, *Caldeira & Marques 595* (LMU, WAG); Sul do Save, Marracuene, between Lourenço Marques and Costa do Sol, Jan., *Pedro & Bachir 3846* (LMA); *Exell et al. s.n.* (LISC); between Vila Luiza and Manhiça, 17 Nov., *Myre & Carvalho 1043* (LMA); Polana Beach, Delagoa Bay, *Thoday 169* (SAM). NAMIBIA. OVAMBOLAND: 17.15 (Ondangua) Ondangua, open sandy flats, 5 Feb. 1959 (DD), *de Winter & Giess 6877* (M, WIND); 1924, *Liljeblad 190* (Z); 17.16 (Enana) Oniipa, eroded field, 7 Mar. 1967 (CC), *Soini 429* (WIND); Olukonda, 30 Jan. 1887, *Rautanen 2* (Z), Feb. 1894 (CC), *Rautanen 170* (B, G, Z); *Schinz 2* and *s.n.* (B, K, Z); 30 Dec. 1885, *Schinz 15* (Z); 18.15 (Okahakana) Onambeke–Onolongo (?BB); Apr. 1923, *Barnard 141* (SAM), *573* (SAM). OKAVANGO: 17.19 (Runtu) 10 km E of Runtu, Jan. 1956 (DD), *Kruger 1* (PRE); 19.20 (Tsumkwe) 15 km E of Tsumkwe on road to Botswana, 10 Jan. 1971 (DA), *Giess et al. 11196* (WIND); Tsumkwe, hard black sand, Oberflachenkalk, 13 Jan. 1971, *Giess et al. 11050* (WIND); Simkue, 157 mi. E of Grootfontein, *Acacia–Combretum* parkland, 17 Jan. 1958 (DB); *Story 6162* (M, PRE, SRGH, WIND). KAPRIVI: 17.24 (Katima Mulilo) Mpilila Island, locally common near marsh, 12 Jan. 1959, *Killick & Leistner 3325* (PRE, SRGH, WIND). REHOBOTH: 23.17 (Rehoboth) farm Arovley, red sand, 14 Feb. 1965 (AA), *Giess 8401B* (M, WIND). MARIENTAL: 25.17 (Gibeon) sandbodem, Sudkalahari bis Gibeon, May 1912 (BA-BB), *Range 1455* (SAM). SOUTH AFRICA. CAPE: 24.20 (Unions End) Kalahari Park, Khaapan, Jan. 1978 (BD), *van der Walt* (PRE); 28.21 (Upington) ca. 40 km N of Upington at the S edge of the Kalahari, 1 Apr. 1980 (AB), *Snijman 235* (NBG); 28.22 (Glen Lyon) sandveld W of Padkloof, on dune running parallel with the Langebergen, 15 Mar. 1937 (DA), *Acocks 2057* (PRE). TRANSVAAL: 24.28 (Nylstroom) Waterberg, Zandrivierspoort near Alma, farm Witpoort, 5 Mar. 1979 (AC), *van Wyk 2680* (M, PRE). ZAMBIA. NORTHERN: Shiwa Ngandu, 17 Jan. 1937, *Ricardo 147* (BM). LUAPULA: Lake Mweru, sandbank above high water mark, 13 Nov. 1957, *Fanshawe 3941* (BR, K, NDO, P). CENTRAL: Serenje District, Kanona, July 1968, *Williamson 1337* (K, MO, PRE, SRGH). SOUTHERN: Mazabuka, Ridgeway road, stony red soil, 2 Dec. 1931, *Trapnell 538* (BR, K, PRE); Machili, 10 Dec. 1960, *Fanshawe 5959* (K, NDO, SRGH); 27 Dec. 1960 (fr), *Fanshawe 6026* (K, NDO, SRGH); 3 mi. from Namwala on Ngama road, 16 Dec. 1962, *van Rensburg 1101* (BR, K, LISC, PRE, SRGH); Namwala, Kalahari, sand in dambo, 3,300 ft., *van Rensburg 2039* (K, SRGH). WESTERN: Barotseland, 6 mi. N of Senaga, moist sandy soil at edge of plains, 1 Aug. 1952, *Codd 7329* (BM, BR, K, MO, PRE, S, SRGH); Kalabo, river bank, 2 Aug. 1962, *Robinson 5437* (K, P, SRGH); Kalabo District, between Sandaula pontoon and Kalabo, edge of grassy floodplain, 12 Nov. 1959, *Drummond & Cookson 6389* (E, K, LISC, MO, SRGH); Mongu, Barotseland, 22 Dec. 1965, *Robinson 6749* (K, M, SRGH, WAG); Sesheke District, no date, *Gairdner 69* (K). ZIMBABWE. MATABELELAND NORTH: Shangani River, NE of Bulawayo, 7 Jan. 1898, *Rand 229* (BM). MASHONALAND EAST: Salisbury, Nov. 1919, *Eyles 1885* (K, PRE, SAM, SRGH); Hunyani District, Old Charter road, 27 Dec. 1926, *Eyles 4622* (S, SRGH); Marandallas, Looe, near stream, 22 Dec. 1948, *Wild 2716* (BR, K, S, SRGH). MIDLANDS: Gwelo, whitewaters dam, *Loveridge 596* (K, SRGH); Charter District, 27 Dec. 1926, *Charter 4622* (K). WITHOUT PRECISE LOCALITY: NAMIBIA: Otjiluo, 3 Dec. 1909, *Dinter 886* (SAM); Onolongo, *Barnard 572* (SAM); Omatako, im omuramba, 14 May 1939, *Volk 2056* (M).

15b. Subsp. littoralis

Lapeirousia caudata subsp. *burchellii* (Baker) Marais & Goldbl., Ann. Bolus Herb. 4: 30–33. 1972. *Lapeirousia burchellii* Baker, Handbk. Irideae 171. 1892; Fl. Cap. 6: 93–94. 1896. TYPE: South Africa. Cape: 26.23 (Morokweng) Chooi Desert, Oct. 1812 (AC), *Burchell 2350* (lectotype, K, designated by Goldblatt, 1972; isolectotypes, G, P).

Lapeirousia ramosissima Dinter, Feddes Rep. 29: 255. 1931. TYPE: Namibia. Lüderitz: dunes near Gründorn, *Dinter 5043* (holotype, B; isotypes, BOL, BR, G, K, PRE, SAM, Z).

Lapeirousia streyi Suesseng., Mitt. Bot. Staatssamml. München [1](3): 88. 1951. TYPE: Namibia. Lüderitz: dunes S of the Kuiseb, *Strey 2587* (holotype, M; isotype, PRE (cited in error as holotype by Goldblatt, 1972)).

Plants 10–15(–20) cm high, usually with 1–several short branches produced from near the base. *Inflorescence* usually a crowded cluster of short spikes, each 4–8-flowered; *bracts* 15–20 (–25) mm long. *Flowers* with a perianth tube 28–35 mm long; *tepals* 13–15 mm long and 2–3 mm wide, not usually filiform even on drying.

Distribution. Subspecies *littoralis* occurs in an arc from a somewhat isolated northern extension in southwestern Angola through western and southern Namibia and the northern Cape Province of South Africa into southern Botswana (Fig. 16). In Namibia it extends from near the Brandberg in the central west to the Lüderitz District in the south. In South Africa subsp. *littoralis* occurs in interior Namaqualand east of Springbok and in the northern Cape.

Additional specimens examined. ANGOLA. NAMIBE: near Mossamedes close to Vila Arriaga, 7 Feb. 1956, *Torre 8824* (LISC). BOTSWANA. NGWAKETSE: 25.25 (Mafekeng) Moropedi ranch, 15 Sep. 1978 (CA), *Hansen 3455* (C, K). NAMIBIA. OMARURU: 21.14 (Uis) Brandberg, B. W. Mine–Uis Mine road, sand in rocky ground, 14 Mar. 1963 (AA), *Kers 942* (WIND); Messumberge, foot of mountains, 19 Mar. 1967 (AC), *Giess 9689* (M, PRE, WIND); Nabab Hill, Brandberg area, 4 Mar. 1978 (AB), *Craven 715a, 715b* (WIND). SWAKOPMUND: 22.15 (Trekkopje) 1 mi. NW of farm Bloemhof (AD), *Giess et al. 5079* (M, WIND); 23.15 (Rostock) Namib Park, Tumasberg at campsite (BA), *Giess 13550* (M, WIND).

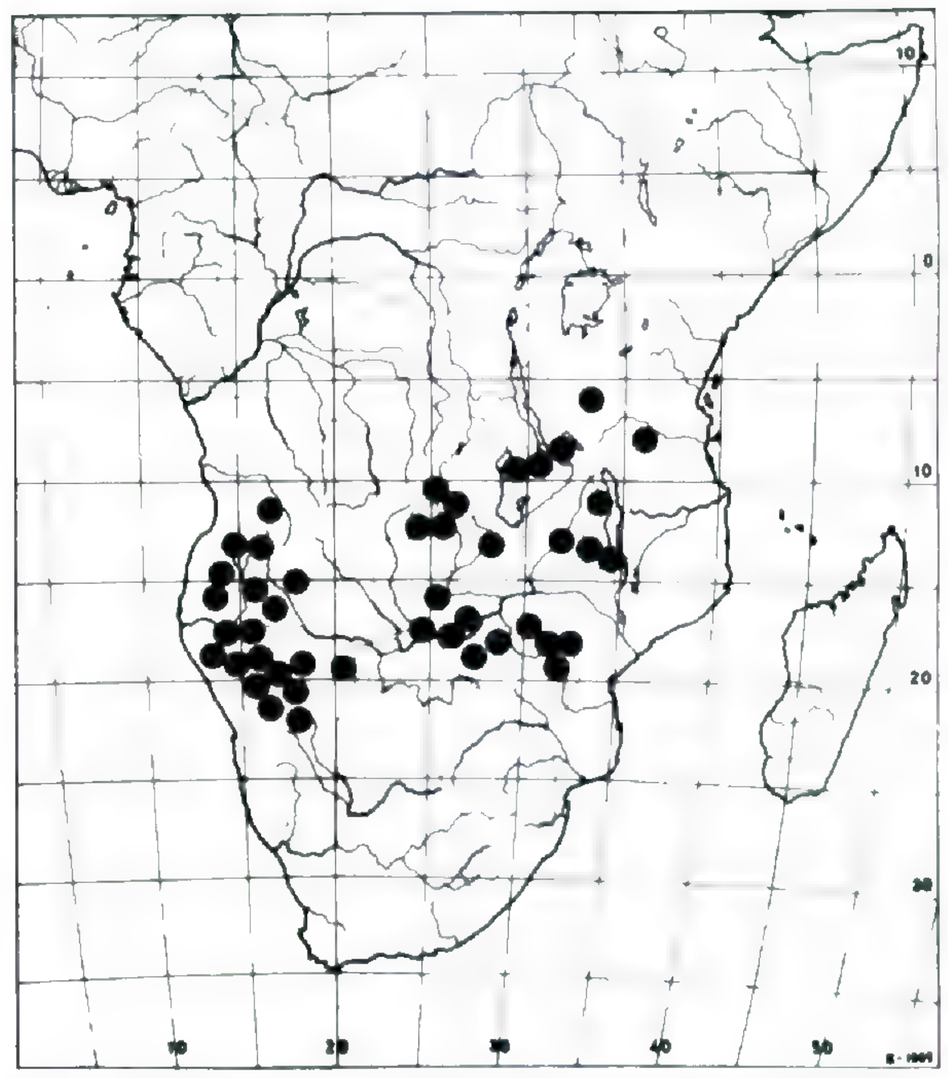

FIGURE 17. Morphology and distribution of *Lapeirousia odoratissima*. Habit and corm × 0.5; detail of stamens and style × 2. (Drawn by J. C. Manning.)

MALTAHÖHE: 25.16 (Helmeringhausen) farm Duwisib, 17 May 1956 (BC), *Volk 12782* (M, MO). LÜDERITZ: 26.16 (Aus) dunes 15 mi. W of Aus (CB), *Giess & van Vuuren 828* (WIND); 13 mi. W of Aus, coarse sand, *Giess & van Vuuren 824* (M, WIND). SOUTH AFRICA. CAPE: 25.20 (Mata-Mata), Kalahari Gemsbok Park, between the Nossob and Auob dunes, 25 Apr. 1960 (BC), *Barnard 807* (PRE); Kalahari Gemsbok Park, 6 mi. SE of Kaffer Pan, loose red sand on dune top, 22 Apr. 1960 (CC), *Leistner 1874* (M, MO, PRE); 26.23 (Morokweng) Chooi Desert, Giraffe Station, Oct. 1812 (AD), *Burchell 2341* (K); 27.18 (Vioolsdrif) Namaqualand, 15 km S of Vioolsdrif, Koubank River, 7 July 1976 (DA), *Giess 14536* (M, WIND); 28.18 (Warmbad) Goodhouse, 27 July 1950 (CD), *Barker 6263* (NBG); 2 mi. S of Goodhouse, 27 July 1950, *Lewis 2272* (SAM); 28.21 (Upington) Upington, sandveld, s.d. (AC), *Mostert 1416* (PRE); 28.24 (Kimberley) 18 mi. SSW of Schmidtsdrift, red sand (CA), 24 Sep. 1961, *Leistner 2866* (B, G, PRE); 29.17 (Springbok) 25 mi. N of Okiep on Goodhouse road (BD), *Lewis 5517* (NBG); 29.18 (Gamoep) Little Bushmanland, Keuzabies (AB), *Schlechter s.n.* or *103* (B, BOL, COI, E, G, MO, P, PRE); Aggenys, 10 mi. W of the farmhouse, 4 Sep. 1971 (BD), *Wisura 2222* (NBG); Ratelkraal, 7 Sep. 1950 (CA), *Barker 6755* (BOL, NBG); 25 mi. E of Springbok, *van Breda 1370* (PRE); 29.19 (Pofadder) 20 mi. from Pofadder on the road to Springbok, *Strauss 123* (NBG).

16. Lapeirousia odoratissima Baker, Trans. Linn. Soc. London (Bot.) ser. 2, 1: 273. 1878; Handbk. Irideae 173. 1892; Fl. Trop. Africa 7: 354. 1897. Sölch, Prod. Fl. Südwestafrika 155: 10. 1969. Geerinck et al., Bull. Soc. Roy. Bot. Belgique 105: 344–346. 1972. TYPE: Angola: sandy woods near Lopollo, *Welwitsch 1551* (lectotype so annotated, BM; isolectotypes, B, BM, C, G, K). Figure 17.

Lapeirousia stenoloba Vaupel, Bot. Jahrb. Syst. 48: 548. 1912. TYPE: Namibia: Omaheke, 1,300 m, in brown sand, 17 Mar. 1911, *Seiner 329* (lectotype designated by Sölch on sheet, B); Omaheke, Jan. 1909, *Dinter 642* (syntype, SAM, as Okanakasura).

Lapeirousia congesta Rendle, J. Linn. Soc. Bot. 30: 435. 1895. Baker, Fl. Trop. Africa 7: 354. 1897. TYPE: Tanzania, "between Zanzibar and Uyui" [the latter near Tabora], *Taylor s.n.* in 1886 (holotype, BM).

Lapeirousia juttae Dinter, Die Vegetabilische Veldkost Deutsch-Südwest-Afrikas 13–14. 1912. TYPE: not cited.

Plants 10–18(–25) cm high, with a condensed aerial axis sometimes rosettelike, rarely the stem partly aerial and with expanded internodes. *Corm* campanulate, 15–20 mm wide at the base, tunics woody, brown, the outer breaking irregularly, rarely becoming fibrous by decay. *Cataphylls* usually 2, the outer one short, the inner reaching almost to ground level, membranous. *Leaves* few, often

only 2 (but hardly distinguishable from the bracts except by position), linear, corrugate, the lowermost inserted below the ground, exceeding the bracts and up to twice as long, to 30 cm long, 3–5 mm wide. *Stem* comprising 1 long basal internode to 8 cm long, usually reaching to just below ground level, upper internodes contracted, rarely 5–10 mm long, the aerial stem 2–5(–10) cm long; simple or with several branches, each subtended by leaves or by leafy bracts. *Inflorescence* comprising 1 or more congested spikes, ± umbellate in appearance, flowers 3–6 per branch; *bracts* herbaceous, 6–15 cm long, lanceolate, the outer lightly corrugate, the inner about ⅓ shorter than the outer, ± membranous. *Flowers* actinomorphic, hypocrateriform, white to ivory, usually strongly scented especially in the evenings; *perianth tube* cylindric, 10–14 cm long; *tepals* narrowly lanceolate, attenuate, 35–40 mm long, extended horizontally or sometimes slightly drooping, widest in the lower third and there 4–5 mm wide. *Filaments* ca. 4 mm long, exserted for 1.5–2 mm, symmetrically disposed; *anthers* 6–8 mm long, linear, white; pollen yellow. *Ovary* ca. 3.5 mm long, *style* usually ultimately reaching to about the apex of the anthers, sometimes shorter, branches 3–4 mm long, forked for ca. half their length, diverging and recurved. *Capsules* obovoid-oblong, 15–18 mm long, concealed in the leaf and bract bases; *seeds* ± globose to somewhat angled by pressure, 2–2.3 mm at the widest diameter. *Chromosome number* $2n = 16$, 18.

Flowering time. December to March, occasionally in April; flowers opening near sunset and white, ivory by morning and gradually wilting during the day.

Distribution and habitat. Although distributed widely across south tropical Africa, *Lapeirousia odoratissima* is apparently common only in Namibia where it occurs most often in sandy flats in the central and upper half of the country. Collections from a number of scattered sites indicate a fairly wide distribution across south tropical Africa except along the east coast and near interior. It extends from southwestern Angola, Zambia, and adjacent Shaba Province of Zaire to central and northern Malawi, Zimbabwe, and in locally dry sites in western and central Tanzania. *Lapeirousia odoratissima* probably also occurs in Botswana although there are no records from that country. Largely a plant of semiarid habitats, *L. odoratissima* also occurs in *Brachystegia* woodland and in exposed places in montane sites, such as the Nyika Plateau in Malawi and the Inyanga Highlands in Zimbabwe, as well as open grassland and *Acacia* savanna.

Little is known about its biology but the large, long-tubed, and usually intensely fragrant flowers are presumably pollinated by hawkmoths. My observations on plants in Namibia indicate that flowers open toward sunset, at which time they are creamy white. By morning the perianth has turned ivory to buff, and the tepals droop slightly below the horizontal; they wilt by the end of the day. The flowers are most intensely fragrant when they first open but maintain their scent through the following day. Ample nectar is produced in the perianth tube. Up to 25 μl was measured in one flower in which the nectar sugar concentration ranged from 16% to 25%. Observations made by Jean Pawek in Malawi confirm my phenological studies: she recorded that buds open between 5:30 P.M. and 6 P.M. but have wilted at least by 10 A.M. (earlier than in Namibia). Flowering phenology is seldom recorded and the presence of fragrance only rarely.

The corms of *Lapeirousia odoratissima* are reported to be edible and to comprise part of the diet of the Khu Bushmen of Namibia (Marshall, 1976).

Diagnosis and relationships. The usual tufted or rosettelike growth habit combined with the large white flowers with an exceedingly long perianth tube 10–14 cm long set *Lapeirousia odoratissima* well apart in the genus. The other tufted to rosette-forming species of sect. *Sophronia* are all southern African and have smaller flowers, colored pale blue to violet. The chromosome number, $2n = 16$ or 18, is the same as in the largely southern African subg. *Lapeirousia* and different from most of the tropical African species with pseudopaniculate inflorescences. Subgenus *Lapeirousia* includes the south tropical African *L. littoralis*, which has somewhat similar white flowers with a shorter but still substantial perianth tube usually 25–45 mm long. *Lapeirousia littoralis* has an aerial stem, and is not likely to be confused with *L. odoratissima*. *Lapeirousia odoratissima* is probably most closely related to *L. littoralis* rather than to the rosettiform southern African species of sect. *Sophronia*.

Flowers very similar to those of *Lapeirousia odoratissima* are found in *L. schimperi* (sect. *Paniculata*), but clearly this species is only distantly related to *L. odoratissima*, and it has the plane leaves and lax pseudopaniculate inflorescence characteristic of sect. *Paniculata*. The long-tubed flowers of these two species are presumably pollinated

by the same agent, most likely a hawkmoth, and are a notable example of convergence in two distantly related species of the same genus.

History. *Lapeirousia odoratissima* was discovered in southern Angola in 1859 by Friedrich Welwitsch, and his collection was described by J. G. Baker in 1878. Another early collection was made by the Rev. W. E. Taylor in central Tanzania in 1886 and was described as *L. congesta* by A. B. Rendle, who distinguished it from *L. odoratissima* on the basis of a more congested habit. Rendle described the plant as having a stem forming a dense sessile head above the first leaf. This is not strictly true, although the internodes of the stem and inflorescence axis are shorter than in the type of *L. odoratissima*, which has among the longest internodes found in the species. From the ample material available it now seems clear that the variation between the extremes represented by the two collections is continuous, and there is no reason to consider them separate species.

Later collections from then German South West Africa made by Kurt Dinter and Franz Seiner were described as *Lapeirousia stenoloba* by Vaupel (1912). He considered these Namibian populations to constitute a species related to *L. odoratissima*, differing by a robust habit and particularly narrow and attenuate tepal apices. Many Namibian specimens of *L. odoratissima* differ from those in tropical Africa by their branched stems and numerous flowers, but intrapopulational variation is considerable in this species, and there are often few-branched or even unbranched plants in populations of more robust ones with several branches, thus the difference does not seem significant taxonomically.

Additional specimens examined. ANGOLA. HUILA: 58 km on road from Sá de Bandeira to Vila Paiva Couceiro, 9 Jan. 1973, *Couto 287* (K, LISC, SRGH); Huila Plateau, dry sandy terrain, Nov.–Dec. 1895, *Berthelot 342* (P); Tchivinguire, 22 Jan. 1962, *Barbosa & Moreno* (COI); Huila, sandy prairies, 1,740 m, Jan. 1899, *Dekindt 733* (LISC, P); Huila, 1883, *Newton 231* (COI, Z); between Huila and Palanca, 26 Jan. 1956, *Mendes 1423* (LISC); Ganguelas, 12 km from Vila Artur toward Galangue, 1,500 m, 5 Jan. 1960, *Mendes 1970* (LISC); Chicungo, ca. 1,700 m, 12 Feb. 1973, *Texeira & Andrade 8446* (LISC). HUAMBO: Benguela Plateau, near River Catumbela near the forte Princeya Amelia Kubango, Sep. 1906, *Gossweiler 99* (K); country of the Ganguellas and Ambuellas, Vila da Ponte, Dec. 1932, *Gossweiler 4022* (COI, K); Mt. Moco, Anhara de Moco (12.15 CD), 19 Dec. 1973, *Huntley et al. 113* (PRE). BIÉ: Andulo, Cruzamento N Lubia a 7 km from Nharea, 1,400 m, 24 Nov. 1965, *Texeira et al. 9518* (LISC). CUNENE: Cuvelai ca. 20 km from Cuvelai to Chamutete, 10 Feb. 1973, *Menezes, Barosso & Sousa 4444* (LISC, SRGH); Cuvelai ca. 16 km from Cuvelai to Bambi, 12 Feb. 1973, *Menezes, Barosso & Sousa 4506* (LISC, SRGH). CUANDO-CUBANGO: Menongue, Caiundo, Capico, near Missão, 1,200 m, 30 Jan. 1960, *Mendes 2234* (LISC). MALAWI. NORTHERN PROVINCE: Mzimba District, 22 mi. W of Mzuzu, Kasitu River, 3,800 ft., 2 Mar. 1974, *Pawek 8611* (MO); Mzimba District, 7 mi. S of Mutini, W toward Rukuru River, ca. 1,260 m, 31 Jan. 1976, *Pawek 10798* (K, MAL, MO); Nyika Plateau, grassland at radio transmitter, 4,100 ft., 19 Feb. 1976, *Phillips 1251* (MO); Mzimba District, 5 mi. W of S49 toward Vuvumwe bridge, 20 Jan. 1978, *Pawek 13642* (BR, MO, SRGH, WAG); Mzimba District, edge of dirt road in sand, behind Ekwendeni, 26 Feb. 1978, *Pawek 13931* (K, MAL, MO); Mzimba District, ca. 10 km N of Mpherembe, *La Croix 4304* (MO). CENTRAL PROVINCE: Chitipa District, Kaseye Mission 10 mi. E of Chitipa, 1,270 m, closed in daytime, 26 Dec. 1977, *Pawek 13376* (K, MAL); Lilongwe-Dzalanyamas road near Ketete bridge, dry sandy dambo, 6 Feb. 1957, *Robson 1483* (BM, K, MAL, PRE, SRGH); Kasungu Game Reserve, white sand, 20 Jan. 1970, *Hall-Martin 577* (PRE); Dowa District, Kongwe Forest Reserve, shallow gravel over rocks with *Xerophyta*, 7 Mar. 1982, *Brummitt et al. 16394* (K). NAMIBIA. KAOKOVELD: 18.13 (Ohopoho) Okakura, 28 Feb. 1913 (DA), *Dinter 3322* (SAM). KAOKOVELD: 19.14 (Kamanjab) N of Otjovasandu in red sand, 11 Mar. 1976 (BA), *Giess & Loutit 14191* (WIND). OUTJO: 19.14 (Kamanjab) Etosha National Park, Kaross, 9 Apr. 1974 (fr) (B-), *Volk & Le Roux 807* (WIND); between Kaross and Kamanyab (BC), *Thorne s.n.* (SAM 313743); 19.15 (Okaukuejo) 10 km W of farm Uitzig, ca. 60 km ENE of Otjiwarongo, grassveld on red sandy loam, 9 Feb. 1983 (CB), *Lavranos & Pehlemann 21059* (MO, WIND). OVAMBOLAND: 17.15 (Ondangua) Ondonga (DD), *Barnard 196* (SAM); 18.15 (Okahakana) Onolongo–Onambeke, Apr. 1923 (?BB), *Barnard 136* (SAM). GROOTFONTEIN: 19.16 (Gobaub) farm Norabis 387, thornveld, 18 Mar. 1988 (fr) (DD), *Goldblatt & Manning 8824* (MO); 19.17 (Tsumeb) Auros (Otavi), 10 Feb. 1925 (DA), *Dinter 5599* (B, G, GH, PRE, SAM, Z); 19.18 (Grootfontein) 30 mi. N of Gautscha Pan, 10 Feb. 1958 (CA), *Story 6460* (PRE); Oliewenhof farm, sandy flats, 8 Mar. 1974 (fr) (CB), *Merxmüller & Giess 30147* (M, WIND). OTJIWARONGO: 20.17 (Waterberg) Otjiwarongo District, farm Okosongomingo, 4 Mar. 1974 (CA), *Merxmüller & Giess 30023* (M, PRE, WAG, WIND). OKAHANDJA: 21.16 (Okahandja) Omatako View, red sand, 4 Mar. 1974 (BA), *Woortman 256* (WIND); 21.17 (Otjosondu) Okahandja District, farm Hochveld, brown sandy loam, 30 Apr. 1963 (fr) (BD), *Giess et al. 6672* (WIND); Okahandja, 22 Feb. 1928 (DD), *Bradfield 385* (PRE). WINDHOEK: 21.17 (Otjosondu) 35 km from Steinhausen to Windhoek on Kapps farm road, 15 Mar. 1988 (DD), *Goldblatt & Manning 8807* (MO); 22.17 (Windhoek) farm Bodenhausen, near the river, 7 Mar. 1959 (BC), *Seydel 1771* (M, WIND). GOBABIS: 19.20 (Tsumkwe) Grootfontein District, ca. 3 mi. S of Nama Pan (DC), *Story 6275* (M, PRE, WIND); 20.20 (Kaukauveld) Kaukauveld, 56 mi. N of Eiseb Omuramba toward Kano Vlei, 13 Apr. 1967 (fr) (AD), *Giess 9815* (WIND); 21.18 (Steinhausen) 15 km from Steinhausen to Windhoek on Kapps Farm road, 15 Mar. 1988 (fr) (CC), *Goldblatt & Manning 8803* (MO). TANZANIA. IRINGA: 12 mi. SE of Iringa, 5,500 ft., well-drained red soil, 8 Feb. 1962, *Polhill & Paulo 1390* (B, BR, K, LISC, P, PRE, SRGH). RUKWA: Sumbawanga, Ufipa, among roadside grasses, 6,300 ft., 29 Jan. 1950,

Bullock 2357 (B, BR, K, MO, S); Ufipa Plateau, *Michelmore 1065* (K). ZAIRE. SHABA: Mamea Plain, 9 Jan. 1938, *Paterson s.n.* (K); plateau de Manika, 12 km SW de Kolwezi, 5 Jan. 1983, *Schaijes 1779* (BR); ca. 2 km W de Katema, 21 Jan. 1969, *Lisowski et al. 179* (BR). ZAMBIA. COPPERBELT: Kasempa District, Chati Forest Reserve, W of Kasempa road, sandy edge of path to dambo, 12 Jan. 1961, *Linley 55* (MO, SRGH); Chati dambo, Jan. 1962, *Odgers 675* (NDO). EASTERN: Luangwa Valley near Mupomadzi River, 2,000 ft., 15 Jan. 1966, *Astle 4415* (K, SRGH). NORTHERN: Mbala District, Mbala, 13 Jan. 1970, *Sanane 984* (K, P); Mbala District, Chenda farm, dam, grassland, 13 Jan. 1965, *Richards 19554* (K); Abercorn–Lunzua Falls road, red sand at top of escarpment, 1,500 m, 26 Jan. 1962, *Richards 15962* (K); Mbala District, road to Inono village, sandy track, 5,000 ft., 18 Jan. 1955, *Richards 4142* (BR, K). NORTHWESTERN: Mwinilunga District, S of Samuteba on Solwezi Mwinilunga road, sandy dambo, 19 Jan. 1975, *Brummitt et al. 13875* (K, NDO, SRGH); Mwinilunga Subdistrict, plain, Feb., *Marks 136* (K). SOUTHERN: Machili, woodland, 22 Dec. 1960, *Fanshawe 5994* (K, NDO, SRGH); Choma, shallow gravel soil in miombo, 20 Jan. 1956, *WRB 235* (NDO); Victoria Falls, 3,000 ft., *Rogers 5393* (K). WESTERN: Barotseland, Moufu, sandy grassland at edge of woodland, 22 Dec. 1965, *Robinson 6749* (WAG); Sesheke, Jan. 1925, *Borle s.n.* (PRE, SRGH). ZIMBABWE. MANICALAND: Inyanga District, Juliasdale, Pteridium grassland W of Punch Rock, in fire break, 1,925 m, 24 Dec. 1972, *Biegel 4122* (K, LISC, MO, PRE, SRGH); Inyanga National Park, near Maroro bridge, 23 Jan. 1975, *Burrows 705* (NBG, SRGH); Inyanga District, sandy level river bank, *Chase 581* (BM, K, SRGH); Inyanga, 6,000 ft., *Bayliss 10641* (MO); Inyanga, grassland along the road, 1,700 m, 13 Jan. 1931, *Fries et al. 4244* (BM, BR, PRE, S); Rusape, 23 Jan. 1939, *Hopkins s.n.* (SRGH 7042); Manica District, Odnani River valley, 1915, *Teague 334* (K). MASHONALAND NORTH: Lomagundi, Audley farm, Darwendale, 24 Jan. 1969, *Biegel 2843* (PRE, SRGH); Bindura, 8 Jan. 1932, *Brain 8063* (SRGH). MASHONALAND EAST: Macheke, 5,000 ft., sweet scent, *Eyles 1989* (K, PRE, SRGH); near Salisbury, Jan. 1912, *Craster 75* (K); Salisbury District, Lake McIlwaine, *Plowes 2548* (BR, K, LISC, PRE, SRGH); Marandellas, dry veld, Dec. 1947, *Dehn 108* (M, SRGH); Marandellas Pasture Station, 16 Jan. 1931, *Rattray 233* (SRGH); Nuza Plateau near Panga, Jan. 1935, *Gilliland 1408* (BM, K). MATEBELELAND NORTH: Victoria Falls, Jan. 1910, *Rogers 5393* (SRGH); Shangani/Bubi District, Gwampa Forest Reserve, Kalahari sand in *Baikiaea* woodland, *Goldsmith 87/56* (K, PRE, LISC, SRGH). MIDLANDS: Gokwe, *Brachystegia* woodland on sand, 2 Feb. 1964, *Bingham 1201* (K, SRGH). WITHOUT PRECISE LOCALITY: NAMIBIA: ?17.14 (AC) Kunene River banks, Mar. 1923, *Barnard 135* (SAM); ?19.15 (BB) Okakuja, Jan. 1912, *Dinter 2574* (BM, K, SAM); Apr. 1912 (fr), *Dinter 2649* (SAM); Mar. 1913, *Dinter 2788* (SAM).

EXCLUDED SPECIES

Lapeirousia graebneriana Harms, Bot. Jahrb. Syst. 28: 366. 1901. TYPE: Tanzania, Uhehe: Ufuagi, 1,800 m, Mar. 1899, *Goetze 748* (holotype, B; isotype, BR) = **Anomatheca laxa (Thunb.) Goldbl.** Fairly typical of the species, with a slender narrow perianth tube, but the bracts are 10–15 mm long, the lower flower with the largest bracts.

Lapeirousia holostachya Baker, Kew Bull. 390. 1894; Fl. Trop. Africa 7: 354. 1897. TYPE: Tanzania. Fwambo, *Carson 14/1893* (holotype, K, not seen). = **Radinosiphon leptostachya (Baker) N. E. Br.** (Carter, Fl. Pl. Africa 35: pl. 1384. 1962).

Lapeirousia welwitschii Baker, Handbk. Irideae 168–169. 1892. TYPE: Angola: Malange, Pungo Andongo, 9°40″ 15°35″, Jan. 1857, *Welwitsch 1531* (BM, annoted as lectotype in unknown hand; isolectotypes, C, COI, G, K, P). The type specimens are poorly preserved, especially the flowers, and as discussed under *L. rivularis*, may be either *L. rivularis* or *L. erythrantha*. The type locality must be visited to resolve this question.

Lapeirousia erythrantha var. *welwitschii* (Baker) Marais ex Geerinck, Lisowski, Malaisse & Symoens, Bull. Soc. Roy. Bot. Belgique 105: 340–341. 1972.

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LÉON CROIZAT'S PLANT COLLECTIONS FROM THE FRANCO-VENEZUELAN EXPEDITION TO THE HEADWATERS OF THE RIO ORINOCO[1]

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and
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ABSTRACT

In 1951 Léon Croizat participated in the Franco-Venezuelan expedition to the headwaters of the Río Orinoco and amassed over 1,000 plant collections, noteworthy because it was the first in that area. Although most of the collections represent widespread riverine species, two new species with restricted distributions have recently been described. We present a brief account of the expedition, a list of Croizat's collections by number and family, and a map illustrating the collecting localities.

Léon Croizat-Chaley (1894–1982) is best known for his writings on biogeography (Croizat, 1952, 1958, 1961), systematics (mainly the Euphorbiaceae), and morphology. Born and raised in Italy, he moved to Venezuela in March 1947 after studying for a few years at the Arnold Arboretum of Harvard University. In Venezuela he held various positions including Professor of Botany and Ecology at the University of the Andes in Mérida, and later Technical Director of the Xerophytic Botanical Garden in the state of Falcón. He was a prolific writer, amassing a bibliography of over 15,000 pages including his monumental *Panbiogeography* (1958), *Principia Botanica* (1961), and *Space, Time, Form: The Biological Synthesis* (1964). Less well known are his plant collecting efforts. In 1951 at the age of 57, Croizat participated as botanist in the Franco-Venezuelan expedition to the headwaters of the Río Orinoco. He was decorated with the "Order of the Liberator" by the Venezuelan government for his contributions to the expedition (Steyermark, 1983).

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We also thank the following people for identifications: W. R. Anderson (MICH), Malpighiaceae; L. Andersson (GB), Musaceae; M. M. Arbo (CTES), Turneraceae; D. F. Austin (FAU), Convolvulaceae; R. Barneby (NY), Caesalpiniaceae, Menispermaceae, Mimosaceae; H. Bedell (GH), Marcgraviaceae; C. C. Berg (BG), Moraceae; B. Boom (NY), Theaceae (*Ternstroemia*); E. Christenson (SEL), Orchidaceae (in part); T. Croat (MO), Araceae; C. Cristóbal (CTES), Sterculiaceae; W. D'Arcy (MO), Solanaceae; C. Dodson (MO), Orchidaceae (in part); A. Gentry (MO), Bignoniaceae; R. Harley (K), Lamiaceae; G. Harling (GB), Cyclanthaceae; A. Henderson (NY), Arecaceae; W. H. A. Hekking (U), Violaceae; R. Howard (A), Polygonaceae; M. Huft (MO), Euphorbiaceae (in part); J. Kallunki (NY), Bombacaceae; H. Kennedy (UBC), Marantaceae; R. Kral (VDB), Xyridaceae; A. Krapovickas (CTES), Malvaceae; K. Kubitzki (HBG), Clusiaceae (*Caraipa*), Dilleniaceae; A. J. M. Leeuwenberg (WAG), Apocynaceae (*Tabernaemontana*); R. Liesner (MO), miscellaneous; J. Luteyn (NY), Ericaceae; P. J. M. Maas (U), Burmanniaceae, Gentianaceae, Triuridaceae, Zingiberaceae; L. Marcano Berti (MER), Vochysiaceae; W. Meijer (KY), Tiliaceae; A. Mennega (U), Hippocrateaceae; J. Mickel (NY), Aspleniaceae (*Elaphoglossum*); J. Miller (MO), Boraginaceae; S. Mori (NY), Lecythidaceae; M. Nee (NY), Amaranthaceae; B. Øllgaard (AAU), Lycopodiaceae; T. Pennington (K), Meliaceae, Sapotaceae; J. Murça Pires (MG), Quiinaceae; T. Plowman (F), Erythroxylaceae; G. Prance (K), Chrysobalanaceae; J. Pruski (NY), Asteraceae; N. K. B. Robson (K), Clusiaceae (*Hypericum, Vismia*); W. A. Rodrigues (INPA), Myristicaceae; P. van Royen, Podostemaceae; L. Skog (US), Gesneriaceae; A. R. Smith (UC), all pteridophytes except *Elaphoglossum* and Lycopodiaceae; C. Stace (LTR), Combretaceae; B. Stein (Nature Conservancy), Campanulaceae; P. Taylor (K), Lentibulariaceae; W. Thomas (NY), Simaroubaceae; S. Tillett (MYF), Passifloraceae; K. Vincent (NY), Scrophulariaceae; D. Wasshausen (US), Acanthaceae; G. Webster (DAV), Euphorbiaceae (in part); A. Weitzman (US), Theaceae (*Freziera*); J. J. Wurdack (US), Melastomataceae, Polygalaceae; H. van der Werff (MO), Lauraceae; E. Zardini (MO), Onagraceae.

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The expedition was conceived by Joseph Grelier, a French geographer and hydrographer, who desired to find the source of the Orinoco. In addition to reaching the headwaters of the Río Orinoco and establishing its coordinates, the objectives of the expedition included contacting the various Indian tribes and making archaeological, anthropological, and ethnographic studies, studying in detail the flora and fauna of the region, investigating the geology of the area, and obtaining photographs to increase the knowledge of the area and serve as a base for future investigations (Contramaestre, 1954).

Grelier recruited two other Frenchmen, Pierre Couret, a pharmacologist and botanist, and Raymond Pélegri, a radio technician, plus Frantz Laforest, a Canadian ethnologist and archaeologist. When the French group arrived in Caracas, the Minister of Defense appointed Major Franz Rísquez-Iribarren to assist in the preparations and to recruit a Venezuelan team. Quickly the expedition grew to include Captain Félix Cardona Puig, his son Félix Cardona Johnson, geologists Marc de Civrieux and Carlos Carmona, archaeologist José-María Cruxent, entomologist and parasitologist Pablo Anduze, Luis Carbonell, René Lichy, and Léon Croizat. In total the expedition involved 54 members, including 14 scientific personnel and 40 assistants and members of the military. Such a large and diverse cast of characters with conflicting interests and personalities resulted in five books, each airing a different viewpoint on the expedition (Anduze, 1958; Contramaestre, 1954; Grelier, 1954, 1957 (English translation); Lichy, 1978; Rísquez-Iribarren, 1962). The five books are similar in that they all provide an account of the expedition and include maps and numerous photographs. Lichy (1978) provided a day-by-day log of the expedition apparently derived from his journal. As military commander of the expedition, Rísquez-Iribarren presented a more technical account including much cartographic information. Anduze (1958) commented on each of the expedition members and provided a narrative of the journey and a long chapter of observations on the Yanomami, an indigenous group in the upper Orinoco region. He included photographs of the personnel on the expedition and of the Yanomami, as well as appendices on the mammals, birds, insects, grasses, and palms collected on the trip. A more loquacious narrative is Grelier's (1954, 1957, 1971), who also provided some historical background as well as photographs of the river and its surroundings. Contramaestre (1954) gave a very brief account with photographs of everyone on the expedition or associated with it. It is mainly from these five books that the following account is drawn.

On April 9, 1951, after four months of preparation in Caracas, expedition members flew from Caracas to San Fernando de Atabapo, closest airstrip to La Esmeralda, to construct a base camp and landing strip. Base Camp Number 1, as La Esmeralda was called, served the dual function of the first study area and the first operational base. In June, Croizat left Caracas along with other members of the expedition by small plane headed for La Esmeralda, but because of bad weather were routed to Puerto Ayacucho. They then traveled by river to La Esmeralda. On this journey of seven days, Croizat collected his first 60 numbers of the expedition.

On the expedition Croizat dressed in khaki garb, a tropical pith helmet, and was well-armed with two knives, a revolver, and a rifle (Lichy, 1978, p. 112). Anduze (1958, p. 48) observed that of all the expedition members Croizat was the most dedicated to documenting the trip and kept very clear and meticulous notes. Unfortunately, his copious notes on the expedition do not survive.

Situated on the north bank of the Orinoco, La Esmeralda is surrounded by a mixture of savanna, forest, and sandstone hills. Croizat and Couret searched this area bringing back plants to their camp, which was constantly cluttered with flowers, fruits, and piles of newspaper and blotting paper. They dried their specimens on a makeshift dryer using a continuously burning fire. Croizat and Couret thus were dubbed the "vestal virgins" by other expedition members (Grelier, 1957, pp. 63–64).

In the early 1950s the Orinoco above Esmeralda was still fairly unknown, and no experienced guides were available. In mid-July after an advance party scouted the area, the expedition moved on to the Guaharibo Rapids where they were to set up the second base and research center. The Guaharibo Rapids are the first major barrier on the Upper Orinoco, and there the river is approximately 150 m wide. Croizat spent 11 days in this area and collected over 200 numbers. Although there must have been many harrowing experiences on the expedition, few specifically mention Croizat. However, one evening Croizat and Couret went in the curiara, the dugout canoe made by the native Indians, above the rapids in search of plants, and as they pulled away from shore, the current sucked them into midstream and hurled them through the rapids.

On August 11, Croizat and four other scientists set off from the Guaharibo Rapids for their next stop, Base Camp 3, Salto Salas, named in honor

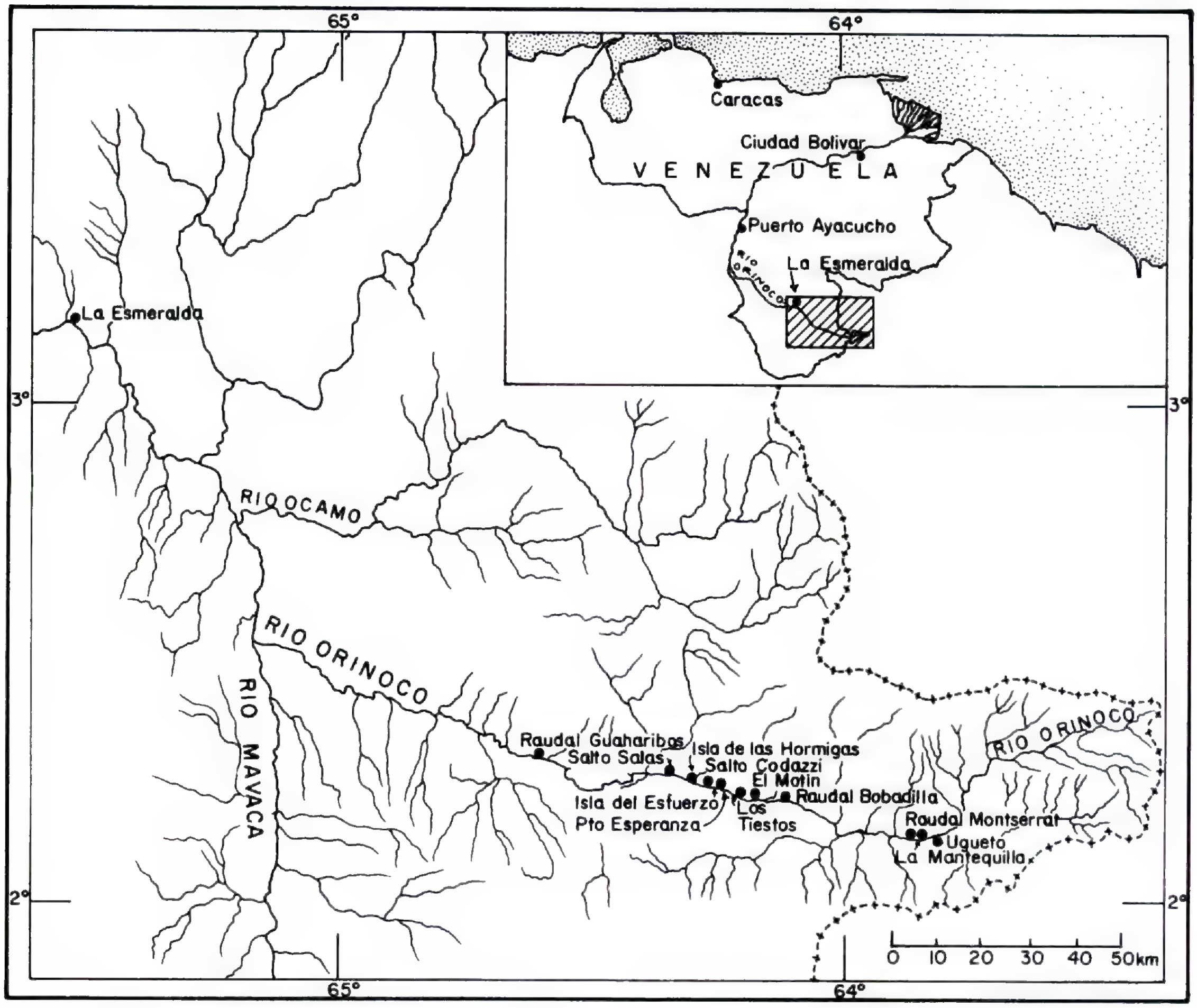

FIGURE 1. Map showing the upper Río Orinoco including Croizat's collecting localities.

of a friend of Major Rísquez. Croizat stayed in the area of Salto Salas for 11 days and collected 84 numbers. Base Camp 4 was established on an island below a broken stretch of water that they named Effort Rapids or Isla del Esfuerzo. It was here that the "Guaharibo Gripe," the fever that had been plaguing the expedition for several weeks, reached epidemic proportions. The constant humidity, fatigue, and necessity of standing in rushing water for long periods of time began to wear on the crew. The camp had as many as 10 sick men at a time. Major Rísquez felt it best that the sick be evacuated at this time, and the first group returned to La Esmeralda where a plane could pick them up. Croizat continued on with the expedition to the next camp, Potsherds, or Los Tiestos, where the expedition stayed for only three days. It was decided that those who were well would form an exploratory group taking 25 men and six boats, continue upriver for seven days, and then send the boats and men back to the main party. On September 11, the party set out, and after an entire day's effort, no more than a mile of river had been traversed. And on that day, to Croizat's despair, the boat carrying the botanical specimens was submerged in water. The party moved upriver slowly, spending nights camped at El Motín, Raudal Bobadilla, El Queso, Raudal Montserrat, localities where Croizat collected specimens. Croizat continued on with the advanced exploratory part to the confluence with the Río Ugueto.

At the mouth of the Río Ugueto, the expedition pitched camp and decided to rest so that each scientist could continue his own research. Here Croizat collected 65 numbers. The rains were beginning to let up and the river started to fall. The expedition once again set off, this time loaded with fresh provisions that had been parachuted in. The river now was only 20 m wide and consisted mostly of rocky shoals. It was decided not to take the boats any further upstream, although it was estimated that the source of the Orinoco was 40 miles

further. In these rapids above Ugueto, Croizat lost his field notebooks and journal (letter from Croizat to J. Steyermark, 14 December 1964). Croizat had been sick for some time with toothaches and gastroenteritis (Anduze, 1958, p. 48). He had become so sick that he needed assistance to dress and to get into his hammock (Grelier, 1954, p. 166). At Ugueto, Croizat decided he would go no further and returned to Esmeralda with a party of three others, a journey of 22 days.

Although Croizat's notes and journal were lost, some insights gleaned from his trip were published in his *Panbiogeography*. "In the Upper Orinoco the riverine forest generally alternates between two main types, one denser and richer in high vegetation in stretches where deep, heavy clays dominate; the other rather more open and lower by canopy holding belts or rocky seams and thinner soil (these belts mark as a rule a rapid)" (Croizat, 1958, 1: 416). Some members of the expedition gave exaggerated reports of the botanical richness of the area: "We know, however, that the botanical collection contains a great number of new species and many others which, though known, had not been previously met with in these latitudes" (Grelier, 1957, p. 182), and "Upon leaving the Raudales Atures and Maipures which are the limit of the zone, we find out that the flora and fauna, mostly endemics, are products of the physical condition of the earth" (Anduze, 1958, p. 165). Croizat, however, noted that few of his plants were endemic and that the flora of the upper Río Orinoco was essentially Amazonian (Croizat, 1958, 1: 755).

After the expedition, a full set (or nearly so) of the plants were assembled at VEN and shipped to the U.S. in 1952 (Couret, 1966). These apparently arrived first at F, but were not accepted for fear that they were improperly removed from Venezuela (Steyermark, pers. comm.). Later, they were accepted by Maguire at NY (Steyermark, pers. comm.) where the bulk of them sat in the backlog until 1984. Duplicate collections of certain families (notably the Pteridophytes) exist at several other herbaria, F, MO, P, and VEN, but it is not known how or when they were distributed. Couret (1966) indicated that 1,200 species were collected, though he was probably referring to the total number of collections and about 5,000 samples, so it is possible that if not already destroyed, additional duplicates may eventually turn up.

As Croizat indicated, the specimens are generally riverine plants and thus widely distributed. However, two new species, *Persea croizatii* van der Werff (Lauraceae) and *Ouratea croizatii* Maguire & Steyerm. (Ochnaceae), have been described, each from a single Croizat collection apparently collected on higher ground away from the river. Several prominent plant families of the region, notably Cyperaceae and Poaceae are absent from the list (Appendix I). It is possible that they were separated from Croizat's collections for study upon return to Caracas. Anduze (1958, appendices 4 and 5) presented lists for these two families in Territorio Federal Amazonas but did not cite specimens.

Not all of the botanical collections of the expedition were made by Croizat. Couret, as was previously mentioned, assisted Croizat at times and also independently gathered cryptogams, which he later sent to P for study (Couret, 1966). After Croizat turned back at Ugueto, Pablo Anduze and Luis Carbonell continued collectings plants (Anduze, 1958, p. 133; Huber & Wurdack, 1984). None of their names, however, appear on the plant labels. Cruxent apparently made a separately numbered collection, also from the area above Ugueto (B. Boom, pers. comm.). As with the Croizat collections, Cruxent's are nearly all deposited at NY.

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APPENDIX I. Croizat collections from the headwaters of the Río Orinoco.

1. NUMERICAL LIST

The collections are arranged numerically by Croizat's collection numbers and are preceded by collecting locality and date. If a specimen differs in locality or date from the heading, or if it has no label information, it is noted immediately below the name. If a collection has more detailed notes than that given for the general locality, these are indicated after the plant name. Question marks before two consecutive numbers indicate either a mixed collection or two different collections given the same number. A question mark after the plant name indicates uncertainty by the determiner.

Many of the locality names used during the expedition, and in many of the books resulting from it, are not accepted by Cartografía Nacional of Venezuela. These include the following: Salto Codazzi, Isla de las Hormigas, Pto. Esperanza, Isla del Esfuerzo, Los Tiestos, El Motin, Raudal Bobadilla, El Queso, Raudal Montserrat, and La Mantequilla. They appear on the map (Fig. 1) only as aids in locating the collecting areas.

PUERTO AYACUCHO, 27 JUNE 1951; O5°40′N, 67°38′W; 80 m elev.

1	*Rudgea maypurensis* Standley	Rubiaceae
5	*Manihot brachyloba* Muell. Arg. ?	Euphorbiaceae
6	*Phyllanthus minutulus* Muell. Arg.	Euphorbiaceae
7	*Chamaecrista desvauxii* var. *triumviralis* H. Irwin & Barneby	Caesalpiniaceae
9	*Schiekia orinocensis* (HBK) Meissn.	Haemodoraceae
10	*Bursera* sp.	Burseraceae
11	*Irlbachia alata* (Aublet) P. Maas subsp. *alata*	Gentianaceae

BETWEEN RÍO ATABAPO (04°03′N, 67°40′W), and LA ESMERALDA (03°10′30″N, 65°32′44″W); 1–6 JULY 1951

12	*Ficus nymphiifolia* P. Miller	Moraceae
13	*Dalechampia affinis* Muell. Arg.	Euphorbiaceae
15	*Solanum* sp.	Solanaceae
16	*Distictella magnoliifolia* (Vahl) Sandw.	Bignoniaceae
17	*Talisia firma* Radlk.	Sapindaceae
18	*Heterostemon mimosoides* Benth.	Caesalpiniaceae
19	*Dalbergia riedelii* (Radlk.) Sandw.	Fabaceae
20	*Dalbergia riedelii* (Radlk.) Sandw.	Fabaceae
22	*Hibiscus furcellatus* Desr.	Malvaceae
23	*Myrcia deflexa* (Poiret) DC.	Myrtaceae
24	*Roucheria calophylla* Planch.	Linaceae
25	*Vismia guianensis* (Aublet) Choisy subsp. *persicoides* Ewan	Clusiaceae
26	*Dichorisandra hexandra* (Aublet) Standley	Commelinaceae
27	*Ocotea cymbarum* HBK	Lauraceae
28	*Posoqueria longiflora* Aublet	Rubiaceae
29		Myrtaceae
30	*Croton trinitatis* Millsp.	Euphorbiaceae
31	*Maprounea guianensis* Aublet	Euphorbiaceae
32	*Corynostylis arborea* (L.) S. F. Blake	Violaceae
33	*Galeandra devoniana* Schomb. ex Lindley	Orchidaceae
34	*Amazonia* sp.	Verbenaceae
35	*Gurania spruceana* Cogn.	Cucurbitaceae
36	*Turnera acuta* Willd.	Turneraceae
37	*Peritassa laevigata* (Hoffsgg.) A. C. Smith	Hippocrateaceae
40	*Psychotria poeppigiana* Muell. Arg. subsp. *barcellana* (Muell. Arg.) Steyerm.	Rubiaceae
41	*Croton cuneatus* Klotzsch	Euphorbiaceae
42	*Psychotria poeppigiana* Muell. Arg. subsp. *barcellana* (Muell. Arg.) Steyerm.	Rubiaceae
43	*Strychnos panurensis* Spr. & Sandw.	Loganiaceae
44	*Talisia firma* Radlk.	Sapindaceae
46	*Mikania micrantha* Kunth	Asteraceae
	no locality, no date	
48	*Passiflora securiclata* Masters	Passifloraceae
49	*Croton trinitatis* Millsp.	Euphorbiaceae
50	*Passiflora vitifolia* HBK	Passifloraceae
51	*Phyllanthus orbiculatus* Rich.	Euphorbiaceae
52	*Phyllanthus* sp.	Euphorbiaceae
	Sta. Bárbara del Orinoco	
53	*Miconia scorpioides* (Schldl. & Cham.) Naud.	Melastomataceae

54	*Chamaecrista desvauxii* var. *mollissima* (Benth.) H. Irwin & Barneby	Caesalpiniaceae
56	*Inga nobilis* Willd.	Mimosaceae
57	*Bixa urucurana* Willd.	Bixaceae
	Sta. Bárbara del Orinoco	
58	*Miconia rufescens* (Aublet) DC.	Melastomataceae
59	*Utricularia subulata* L.	Lentibulariaceae
60	*Dipteryx punctata* (Blake) Amshoff	Caesalpiniaceae
	San José	

LA ESMERALDA, 9–20 JULY 1951; 03°10′30″N, 65°32′44″W; 120 m elev.

61	*Ocotea* sp.	Lauraceae
63	*Byrsonima crassifolia* (L.) HBK	Malpighiaceae
64	*Alchornea discolor* Poeppig	Euphorbiaceae
65	*Heteropterys atabapensis* W. R. Anderson	Malpighiaceae
66	*Ladenbergia lambertiana* (A. Braun ex C. Martius) Klotzsch	Rubiaceae
	no locality, no date	
69	*Cassytha filiformis* L.	Lauraceae
70	*Irlbachia pratensis* (Kunth) Cobb & P. Maas	Gentianaceae
71	*Habenaria leprieuri* Reichb.f.	Orchidaceae
72	*Remijia hispida* Spruce ex Schumann	Rubiaceae
74	*Calathea inocephala* (Kuntze) Kennedy & Nicolson	Marantaceae
76	*Polygala subtilis* HBK	Polygalaceae
81	*Piriqueta* sp.	Turneraceae
82	*Psychotria egensis* Muell. Arg.	Rubiaceae
83	*Palicourea calophylla* A. DC.	Rubiaceae
84	*Sipanea hispida* Benth. ex Wernham var. *hispida*	Rubiaceae
85	*Borreria latifolia* (Aublet) Schumann var. *latifolia*	Rubiaceae
86	*Sipanea pratensis* Aublet var. *dichotoma* (HBK) Steyerm.	Rubiaceae
87	*Psychotria bracteocardia* (A. DC.) Muell. Arg.	Rubiaceae
90		Clusiaceae
91	*Crotalaria sagittalis* L.	Fabaceae
92	*Curtia tenuifolia* (Aublet) Knobl. subsp. *tenuifolia*	Gentianaceae
93	*Polygala hygrophila* HBK	Polygalaceae
94	*Polygala hygrophila* HBK	Polygalaceae
95	*Polygala adenophora* DC. var. *robusta* Chodat	Polygalaceae
96	*Meriania urceolata* Triana	Melastomataceae
97	*Passiflora nitida* HBK	Passifloraceae
99	*Tococa macrophysca* Spruce ex Triana	Melastomataceae
100	*Pterogastrus divaricata* (Bonpl.) Naud.	Melastomataceae
106	*Vismia laxiflora* Reichardt	Clusiaceae
108	*Buchnera palustris* (Aublet) Spreng.	Scrophulariaceae
110	*Phyllanthus hyssopifolioides* Kunth	Euphorbiaceae
112	*Burmannia bicolor* C. Martius	Burmanniaceae
113	*Macairea thyrsiflora* DC.	Melastomataceae
116	*Lippia* sp.	Verbenaceae
117	*Bifrenaria longicornis* Lindley	Orchidaceae
118	*Dichaea brachypoda* Reichb.f.	Orchidaceae
119	*Epidendrum nocturnum* Jacq.	Orchidaceae
120	*Passiflora foetida* L. var. *foetida*	Passifloraceae
?121	*Microgramma tecta* (Kaulf.) Alston	Polypodiaceae
?121	*Metaxya rostrata* (HBK) Presl	Metaxyaceae
122	*Lycopodiella caroliniana* (L.) Pichi-Serm. var. *meridionalis* (Underw. & Lloyd) B. Øllg. & Wind.	Lycopodiaceae
123	*Lindsaea stricta* (Sw.) Dryander	Dennstaedtiaceae
124	*Lycopodiella camporum* B. Øllg. & Wind.	Lycopodiaceae
125	*Monotagma laxum* (Poeppig & Endl.) Schum.	Marantaceae
126	*Byttneria genistella* Triana & Planchon	Sterculiaceae
127	*Abolboda macrostachya* Spruce ex Malme var. *macrostachya*	Xyridaceae
130	*Clidemia hirta* (L.) Don var. *tiliifolia* (DC.) Macbride	Melastomataceae
131	*Bellucia grossularioides* (L.) Triana	Melastomataceae
132		Marcgraviaceae
133	*Phyllanthus* aff. *lindbergii* Muell. Arg.	Euphorbiaceae
134	*Acosmium nitens* (J. Vogel) Yakovlev	Fabaceae
135	*Tococa nitens* (Benth.) Triana	Melastomataceae
136	*Clidemia rubra* (Aublet) C. Martius	Melastomataceae
144	*Selaginella parkeri* (Hook. & Grev.) Spring	Selaginellaceae
	Raudal de los Guaharibos, Foot of Mt. Rimbaud, 30 July 1951	

145	*Hirtella racemosa* Lam. var. *hexandra* (Willd. ex Roemer & Schultes) Prance	Chrysobalanaceae
147	*Tetracera willdenowiana* Stued. subsp. *willdenowiana*	Dilleniaceae
148	*Humiria balsamifera* (Aublet) St. Hil.	Humiriaceae
149	*Utricularia amethystina* St. Hil.	Lentibulariaceae
150	*Comolia veronicifolia* Benth. s.l.	Melastomataceae
153		Clusiaceae
154	*Ormosia coccinea* Jackson	Fabaceae
155		Clusiaceae
156	*Phaseolus linearis* HBK	Fabaceae
157	*Vochysia* sp.	Vochysiaceae
157-A	*Ruizterania rubiginosa* (Stafl.) Marcano-Berti Raudal de los Guaharibos, toward the top of Mt. Rimbaud, 30 July 1951	Vochysiaceae
158	*Jacquemontia tamnifolia* (L.) Griseb.	Convolvulaceae
159	*Calycobolus glaber* (HBK) House	Convolvulaceae
161	*Sauvagesia ramosa* (Gleason) Sastre	Ochnaceae
162	*Catasetum discolor* Lindley?	Orchidaceae
?163	*Brassavola martiana* Lindley	Orchidaceae
?163	*Quassia amara* L.	Simaroubaceae
164	*Lindsaea* cf. *portoricensis* Desv.	Dennstaedtiaceae
165	*Trichomanes pilosum* Raddi	Hymenophyllaceae
166	*Heteropterys nervosa* A. Juss.	Malpighiaceae
?167	*Actinostachys pennula* (Sw.) Hook.	Schizaeaceae
?167		Burseraceae
168	*Melochia villosa* (Mill.) Fawcett & Rendle var. *villosa*	Sterculiaceae
169	*Monotrema xyridoides* Gleason	Rapateaceae
170	*Vismia japurensis* Reichardt	Clusiaceae
171		Clusiaceae
172	*Smilax* sp.	Liliaceae
174		Flacourtiaceae
175	*Doliocarpus dentatus* (Aublet) Standley subsp. *esmeraldae* (Steyerm.) Kubitzki	Dilleniaceae
176	*Solanum pensile* Sendtner	Solanaceae
177	*Xylopia aromatica* (Lam.) C. Martius	Annonaceae
178	*Buchnera rosea* Kunth	Scrophulariaceae
180	*Iriartella setigera* (C. Martius) H. A. Wendl.	
183	*Catasetum pileatum* Reichb.f.	Orchidaceae
184	*Ischnosiphon cannoideus* L. Anderss.	Marantaceae
186	*Genipa spruceana* Steyerm.	Rubiaceae
187	*Drosera* sp.	Droseraceae
188	*Pitcairnia patentiflora* Lyman B. Smith var. *patentiflora*	Bromeliaceae
189	*Piriqueta cistoides* (L.) Griseb.	Turneraceae
191	*Chamaecrista desvauxii* var. *brevipes* (Benth.) H. Irwin & Barneby	Caesalpiniaceae
192	*Marsdenia rubrofusca* Benth. ex. Fourn.	Asclepiadaceae
199	*Catasetum discolor* Lindley	Orchidaceae
200	*Tibouchina spruceana* Cogn.	Melastomataceae
201	*Miconia scorpioides* (Schldl. & Cham.) Naud.	Melastomataceae
203	*Macairea thyrsiflora* DC. s.l.	Melastomataceae
204	*Melochia villosa* (Miller) Fawcett & Rendle var. *villosa*	Sterculiaceae
205		Clusiaceae
206	*Epidendrum* sp.	Orchidaceae
207	*Melochia villosa* (Miller) Fawcett & Rendle	Sterculiaceae
208	*Anthurium bonplandii* Bunting subsp. *bonplandii*	Araceae
209	*Psychotria poeppigiana* Muell. Arg. subsp. *barcellana* (Muell. Arg.) Steyerm.	Rubiaceae
210		Burseraceae
211	*Irlbachia alata* (Aublet) P. Maas subsp. *angustifolia* (Kunth) Pers. & P. Maas	Gentianaceae
212	*Cephalostemon affinis* Koern.	Rapateaceae
213	*Gonzalagunia dicocca* Cham. & Schldl. subsp. *dicocca* var. *guianensis* Steyerm.	Rubiaceae
214	*Guatteria* cf. *maypurensis* Kunth Ledges of Cerro Bandera	Annonaceae
215	*Phyllanthus hyssopifolioides* Kunth	Euphorbiaceae
218	*Rhynchanthera grandiflora* (Aublet) DC.	Melastomataceae
221	*Cupania scrobiculata* Rich.	Sapindaceae
224	*Ocotea* sp.	Lauraceae
225	*Psychotria bahiensis* A. DC. var. *cornigera* (Benth.) Steyerm.	Rubiaceae

226	*Siparuna guianensis* Aublet	Monimiaceae
228	*Pagamea coriacea* Spruce ex Benth.	Rubiaceae
229	*Drosera* sp. Cerro de la Bandera	Droseraceae
230	*Cochlospermum orinocense* (Kunth) Steudel no locality, 24 July 1951	Cochlospermaceae
231	*Duckeëlla pauciflora* Garay Cerro de la Bandera	Orchidaceae
232	*Acacallis cyanea* Lindley Cerro de la Bandera	Orchidaceae
233	*Curculigo scorzonerifolia* (Lam.) Baker	Amaryllidaceae
235	*Clidemia capitellata* (Bonpl.) Don var. *dependens* (Don) Macbride Cerro de la Bandera	Melastomataceae
236	*Bredemeyera lucida* (Benth.) A. W. Bennett Cerro de la Bandera	Polygalaceae
237	*Guarea pubescens* (Rich.) A. Juss. subsp. *pubescens*	Meliaceae
237-A	Raudal de los Guaharibos, 21 July 1951	Meliaceae
238	Retiniphyllum schomburgkii (Benth.) Muell. Arg. subsp. *occidentale* Steyerm.	Rubiaceae
239	*Chamaecrista orenocensis* (Benth.) H. Irwin & Barneby Slopes of Cerro Bandera	Caesalpiniaceae

RAUDAL DE LOS GUAHARIBOS, 21 JULY–1 AUG. 1951; 02°18′N, 64°39′W; 150 m elev.

Note: The locality names listed below for some collections, Mt. Rimbaud and Mt. Maunoir, though not officially recognized, correspond to peaks in the Sierra Guaharibo, a mountain range stretching along the Orinoco River to the north of Raudal de los Guaharibos.

241	*Hiraea faginea* (Sw.) Niedenzu	Malpighiaceae
242	*Casearia sylvestris* Sw. La Esmeralda, 21 July 1951	Flacourtiaceae
243	*Apinagia staheliana* (Went) van Royen	Podostemaceae
244	*Hylocereus* sp.	Cactaceae
245	*Heteropterys orinocensis* (HBK) A. Juss.	Malpighiaceae
246	*Lindackeria paludosa* (Benth.) Gilg Between La Esmeralda and Raudal de Los Guaharibos	Flacourtiaceae
248	*Selaginella asperula* Spring	Selaginellaceae
249	*Catasetum barbatum* Lindley	Orchidaceae
252	*Ficus matiziana* Dugand	Moraceae
253	*Miconia* cf. *brevipes* Benth.	Melastomataceae
255	*Xiphidium coeruleum* Aublet	Haemodoraceae
256	*Passiflora vespertilio* L. Salto Salas, 23 Aug. 1951	Passifloraceae
257	*Passiflora longiracemosa* Ducke	Passifloraceae
258	*Selaginella parkeri* (Hook. & Grev.) Spring	Selaginellaceae
259	*Anthurium gracile* (Rudge) Schott	Araceae
260	*Cattleya violacea* (HBK) Rolfe	Orchidaceae
261	*Dichorisandra hexandra* (Aublet) Kuntze Between La Esmeralda and Raudal de los Guaharibos, 23 July 1951	Commelinaceae
262	*Operculina sericantha* (Miq). Ooststr.	Convolvulaceae
263	*Bauhinia glabra* Jacq.	Caesalpiniaceae
264	*Clidemia dentata* Don	Melastomataceae
266	*Clidemia hirta* (L.) Don var. *tiliifolia* (DC.) Macbride	Melastomataceae
267	*Annona* sp.?	Annonaceae
271	*Matayba* aff. *opaca* Radlk.	Sapindaceae
271-A	*Pachira aquatica* Aublet?	Bombacaceae
273	*Cattleya* sp.	Orchidaceae
274		Clusiaceae
275	*Asplenium claussenii* Hieron.?	Aspleniaceae
276		Burseraceae
277	*Pteris propinqua* Agardh	Adiantaceae
278	Mixed collection: *Monstera adansonii* Schott + *Monstera dubia* (HBK) Engl.	Araceae
279	*Voyria flavescens* Griseb.	Gentianaceae
281	*Tournefortia cuspidata* HBK	Boraginaceae

282	*Couepia guianensis* subsp. *guianensis* (Miq.) Prance	Chrysobalanaceae
282-bis	*Inga* sp.	Mimosaceae
283	*Crotalaria micans* Link	Fabaceae
284	*Siparuna guianensis* Aublet	Monimiaceae
285	*Microgramma persicariifolia* (Schrader) C. Presl	Polypodiaceae
286	*Hyptis atrorubens* Poit.	Lamiaceae
289		Araceae
290	*Dioscorea* sp.	Dioscoreaceae
291	*Costus guanaiensis* Rusby var. *macrostrobilus* (Schumann) P. Maas	Zingiberaceae
292	*Costus scaber* Ruíz Lopez & Pavón	Zingiberaceae
293	*Mansoa kerere* (Aubl.) A. Gentry	Bignoniaceae
295	*Adiantum cayennense* Willd. ex Klotzsch	Adiantaceae
296	*Paullinia novemalata* Uitt.	Sapindaceae
297	*Ludwigia latifolia* (Benth.) H. Hara	Onagraceae
298	*Ficus* sp.	Moraceae
300	*Cydista aequinoctialis* (L.) Miers	Bignoniaceae
301	*Mikania guaco* Kunth	Asteraceae
	no locality, no date	
303	*Triplaris americana* L.	Polygonaceae
303-A	*Polygonum acuminatum* HBK	Polygonaceae
304	*Lantana* sp.	Verbenaceae
304-A	*Stachytarpheta* sp.	Verbenaceae
306	*Securidaca* cf. *warmingiana* Chodat	Polygalaceae
307	*Geophila repens* (L.) I. M. Johnston	Rubiaceae
308	Mixed collection:	
	Lindernia dubia (L.) Pennell var. *dubia* + *Scoparia dulcis* L.	Scrophulariaceae
309	*Phaseolus campestris* C. Martius	Fabaceae
310	*Polygala spruceana* A. W. Bennett	Polygalaceae
	La Esmeralda, 24 July 1951	
311	*Tragia volubilis* L.	Euphorbiaceae
312	*Coussapoa* sp.	Moraceae
313	*Hyptis dilatata* Benth.	Lamiaceae
	no locality, no date	
?315	*Thelypteris hispidula* (Decne.) C. Reed	Thelypteridaceae
?315	*Cyclopeltis semicordata* (Sw.) J. Sm.	Aspleniaceae
	no locality, no date	
317	*Jacaranda obtusifolia* subsp. *rhombifolia* (G. Mey) A. Gentry	Bignoniaceae
318	*Monstera dubia* (HBK) Engl.	Araceae
320	*Clavija lancifolia* Desf.	Theophrastaceae
321	*Picramnia latifolia* Tul.	Simaroubaceae
322	*Clibadium* sp.	Asteraceae
323	*Apeiba* cf. *albiflora* Ducke	Tiliaceae
?324	*Hamelia patens* Jacq. var. *glabra* Oersted	Rubiaceae
?324	*Utricularia triloba* Benj.	Lentibulariaceae
	no locality, no date	
325	*Guarea pubescens* (Rich.) A. Juss. subsp. *pubescens*	Meliaceae
327	*Miconia ciliata* (Rich.) DC.	Melastomataceae
330	*Croton palanostigma* Klotzsch	Euphorbiaceae
331	*Philodendron smaragdinum* Bunting	Araceae
333	*Montrichardia linifera* (Arruda) Schott	Araceae
334	*Selaginella umbrosa* Lem. ex Hieron.	Selaginellaceae
335	*Tynanthus polyanthus* (Bureau) Sandw.	Bignoniaceae
337	*Scoparia dulcis* L.	Scrophulariaceae
338	*Inga bourgonii* (Aublet) DC.	Mimosaceae
338-bis	*Inga edulis* C. Martius	Mimosaceae
339	*Pithecellobium* (*Zygia*) *divaricatum* Benth.	Mimosaceae
340	*Wulffia stenoglossa* (Cass.) DC.	Asteraceae
341	*Eupatorium* (*Chromolaena*) *odoratum* L.	Asteraceae
	no locality, no date	
342	*Cochlospermum orinocense* (Kunth) Steudel	Cochlospermaceae
343	*Coussapoa asperifolia* Trécul subsp. *magnifolia* (Trécul) Akkerm. & C. C. Berg	Moraceae
345	*Senna silvestris* (Vell. Conc.) H. Irwin & Barneby	Caesalpiniaceae
346	*Erythroxylum divaricatum* Peyr.	Erythroxylaceae
347	*Tectaria incisa* Cav.	Aspleniaceae
348	*Cissus erosa* Rich.	Vitaceae
348-A	*Cissus sicyoides* L.	Vitaceae

349	*Sauvagesia erecta* L.	Ochnaceae
350	*Byttneria divaricata* Benth.	Sterculiaceae
352	*Vanilla pompona* Schiede	Orchidaceae
353	*Renealmia alpinia* (Rottb.) P. Maas	Zingiberaceae
355	*Guettarda divaricata* (Humb. & Bonpl. ex Roemer & Schultes) Standley	Rubiaceae
356	*Bunchosia decussiflora* W. R. Anders.	Malpighiaceae
357	*Clonodia complicata* (HBK) W. R. Anders.	Malpighiaceae
358	*Selaginella parkeri* (Hook. & Grev.) Spring	Selaginellaceae
358-bis	*Microgramma megalophylla* (Desv.) Sota Los Tiestos, no date	Polypodiaceae
360	*Aciotis indecora* (Bonpl.) Triana var. *macrophylla* Cogn.	Melastomataceae
361	*Aristolochia* sp.	Aristolochiaceae
363		
364	*Cordia nodosa* Lam.	Boraginaceae
365	*Campylocentrum poeppigii* (Reichb.f.) Rolfe	Orchidaceae
366	*Theobroma cacao* L.	Sterculiaceae
367	*Doliocarpus major* Gmel. subsp. *major*	Dilleniaceae
368		Clusiaceae
369	*Geonoma* sp. no locality, no date	Arecaceae
371	*Cordia polycephala* (Lam.) I. M. Johnston	Boraginaceae
372		Burseraceae
373	*Triplophyllum funestrum* (Kunze) Holttum	Tectariaceae
375	*Combretum rotundifolium* Rich.	Combretaceae
376	*Leandra solenifera* Cogn.	Melastomataceae
377	*Arrabidaea pubescens* (L.) A. Gentry	Bignoniaceae
378	*Tetrapterys mucronata* Cav.	Malpighiaceae
379	*Adenocalymma inundatum* var. *surinamensis* Bureau & Schumann	Bignoniaceae
380	*Dalechampia magnoliifolia* Muell. Arg.	Euphorbiaceae
?381	*Philodendron smaragdinum* Bunting	Araceae
?381	*Mimosa myriadena* Benth.	Mimosaceae
383	*Selaginella flagellata* Spring	Selaginellaceae
384	*Turnera odorata* Urban	Turneraceae
385	*Psychotria horizontalis* Sw.	Rubiaceae
386	*Disciphania ernstii* Eichler var. *ernstii* no locality, no date	Menispermaceae
387	*Diodia ocimifolia* (Willd.) Bremek.	Rubiaceae
389	*Calathea propinqua* (Poeppig & Endl.) Koen.	Marantaceae
391	*Rollinia exsucca* (Dunal) A. DC.	Annonaceae
391-A	*Cymbopetalum brasiliense* (Vell. Conc.) Benth.	Annonaceae
392	*Solanum stramonifolium* Vahl	Solanaceae
392-A	*Cestrum latifolium* var. *tenuiflorum* (HBK) O. Schulz	Solanaceae
393		Burseraceae
396	*Philodendron smaragdinum* Bunting	Araceae
397	*Sterculia* sp.	Sterculiaceae
397-A	*Byttneria divaricata* Benth. no locality, no date	Sterculiaceae
398	*Inga edulis* C. Martius	Mimosaceae
398-bis	*Inga leiocalycina* Benth.	Mimosaceae
399	*Costus guanaiensis* Rusby var. *macrostrobilus* (K. Sch.) P. Maas	Zingiberaceae
399-A		Menispermaceae
400	*Philodendron smaragdinum* Bunting	Araceae
401	*Ludwigia leptocarpa* (Nutt.) H. Hara	Onagraceae
405	*Triplophyllum funestrum* (Kunze) Holttum	Tectariaceae
406	*Strychnos matogrossensis* S. Moore	Loganiaceae
407	*Hibiscus bifurcatus* Cav.	Malvaceae
408	*Vanilla palmarum* Lindley	Orchidaceae
408-A	*Vanilla palmarum* Lindley	Orchidaceae
409	*Dichorisandra hexandra* (Aublet) Kuntze	Commelinaceae
410	*Stromanthe* aff. *jacquinii* (Roemer & Schultes) Kennedy & Nicolson	Marantaceae
411	*Renealmia aromatica* (Aublet) Griseb.	Zingiberaceae
412	*Inga stipularis* DC. no locality, no date	Mimosaceae
413	*Acalypha villosa* Jacq.	Euphorbiaceae
414	*Iresine diffusa* Willd.	Amaranthaceae
415	*Oxalis* sp.	Oxalidaceae
416	*Geophila repens* (L.) I. M. Johnston	Rubiaceae

417	*Solanum stramonifolium* Vahl	Solanaceae
418	*Metaxya rostrata* (HBK) Presl	Metaxyaceae
419	*Caladium bicolor* (Aiton) Vent.	Araceae
419-A		Araceae
	Salto Salas, 18 Aug. 1951	
420	*Renealmia alpinia* (Rottb.) P. Maas	Zingiberaceae
421	*Piper aequale* Vahl	Piperaceae
422	*Agarista duckei* (Huber) Judd	Ericaceae
	Upper ranges of Mt. Rimbaud	
423	*Hamelia patens* Jacq. var. *glabra* Oersted	Rubiaceae
426		Family Indet.
	Slopes of Mt. Rimbaud	
427	*Epiphyllum phyllanthus* (L.) Haw.	Cactaceae
	Slopes toward the top of Mt. Rimbaud	
429	*Nautilocalyx* sp.	Gesneriaceae
	Slopes of Mt. Rimbaud	
430	*Isertia parviflora* Vahl. var. *parviflora*	Rubiaceae
	Forest toward Mr. Rimbaud	
432	*Codonanthe crassifolia* (Focke) Morton	Gesneriaceae
	Forest toward slopes of Mt. Rimbaud	
433	*Inga nobilis* Willd.	Mimosaceae
434	*Dicranopteris flexuosa* (Schrader) L. Underw.	Gleicheniaceae
	About 3 hours navigation upstream	
435	*Thibaudia nutans* Mansf.	Ericaceae
	Near summit of Mt. Rimbaud	
437	*Clidemia umbonata* DC.	Melastomataceae
	Foot of Mt. Rimbaud	
438	*Clidemia capitata* Benth.	Melastomataceae
	Forest toward Mt. Maunoir	
439	*Palicourea* aff. *crocea* (Sw.) Roemer & Schultes	Rubiaceae
	Mt. Rimbaud	
440		Lauraceae
441	*Selaginella parkeri* (Hook. & Grev.) Spring	Selaginellaceae
	Foot of Mt. Rimbaud	
442	*Ternstroemia punctata* (Aublet) Sw.	Theaceae
	Toward summit of Mt. Rimbaud	
443	*Polypodium bombycinum* Maxon	Polypodiaceae
	Toward Mt. Maunoir	
444	*Xiphidium coeruleum* Aublet	Haemodoraceae
?445	*Monstera obliqua* Miq.	Araceae
	Isla de las Hormigas, 30 Aug. 1951	
?445	*Aegiphila integrifolia* (Jacq.) Jacq.	Verbenaceae
	Toward Mt. Rimbaud	
446	*Tillandsia adpressiflora* Mez	Bromeliaceae
447	*Cyrilla racemiflora* L.	Cyrillaceae
	Upper ranges of Mt. Rimbaud	
448	*Ernestia tenella* (Bonpl.) DC.	Melastomataceae
	Vicinity of Mt. Rimbaud	
449	*Cyrilla racemiflora* L.	Cyrillaceae
	Rocky slopes of Mt. Rimbaud	
450	*Huperzia linifolia* (L.) Trev. St. Léon. var. *jenmanii* (Underw. & Lloyd) B. Øllg. & Wind.	Lycopodiaceae
451	*Duroia eriopila* L.f. var. *eriopila*	Rubiaceae
451-bis	*Inga nobilis* Willd.	Mimosaceae
452	*Cyrilla racemiflora* L.	Cyrillaceae
	Rocky slopes of Mt. Maunoir	
453	*Anthurium sinnuatum* Benth.	Araceae
	Salto Salas, 1 Aug. 1951	
454	*Ficus* vs. *trigonata* L.	Moraceae
	Salto Salas, 1 Aug. 1951	
455	*Thibaudia nutans* Mansf.	Ericaceae
	Upper range of Mt. Maunoir	
456	*Microgramma persicariifolia* (Schrader) C. Presl	Polypodiaceae
457	*Vellozia tubiflora* (A. Rich.) HBK	Velloziaceae
	Top of Mt. Maunoir	
458	*Navia* sp.	Bromeliaceae
	Slopes of Mt. Maunoir	

SALTO SALAS, 10–21 AUG. 1951; 02°16′N, 64°19′W, ca. 150 m. elev.

459	*Spathiphyllum canniifolium* (Dryander) Schott	Araceae
460	*Mikania psilostachya* DC.	Asteraceae
	no locality, no date	
463	*Miconia ceramicarpa* DC.	Melastomataceae
464	*Ficus guianensis* Desv.	Moraceae
465	*Rollinia exsucca* (Dunal) A. DC.	Annonaceae
466	*Erythrochiton brasiliensis* Nees & C. Martius	Rutaceae
467	*Stromanthe* aff. *jacquinii* (Roemer & Schultes) Kennedy & Nicolson	Marantaceae
468	*Polypodium bombycinum* Maxon	Polypodiaceae
469	*Paullinia* sp.	Sapindaceae
470	*Drymonia serrulata* (Jacq.) C. Martius	Gesneriaceae
471	*Coccoloba latifolia* Lam.	Polygonaceae
472	*Celtis iguanea* (Jacq.) Sarg.	Ulmaceae
473	*Piper arboreum* Aublet	Piperaceae
474	*Erythrina mitis* Jacq.	Fabaceae
475	*Selaginella umbrosa* Lem. ex Hieron.	Selaginellaceae
476	*Pouteria ? plicata* Penn.	Sapotaceae
477	*Rudgea stipulacea* (A. DC.) Steyerm.	Rubiaceae
478	*Psychotria calviflora* Steyerm.	Rubiaceae
479	*Trichilia ? pallida* Sw.	Meliaceae
480	*Iresine diffusa* Willd.	Amaranthaceae
482	*Adiantum pulverulentum* L.	Adiantaceae
483	*Monstera obliqua* Miq.	Araceae
484	*Trichomanes pinnatum* Hedwig	Hymenophyllaceae
485	*Blechnum serrulatum* Rich.	Blechnaceae
486	*Adiantum latifolium* Lam.	Adiantaceae
487	*Trichomanes pinnatum* Hedwig	Hymenophyllaceae
488	*Erythroxylum vernicosum* O. Schulz	Erythroxylaceae
489	*Asplenium serratum* L.	Aspleniaceae
490	*Pityrogramma calomelanos* (L.) Link	Adiantaceae
491	*Dichorisandra hexandra* (Aublet) Standley	Commelinaceae
492	*Astrocaryum gynacanthum* C. Martius	Arecaceae
	no locality, no date	
493	*Paphinia cristata* Lindley	Orchidaceae
494	*Piper demeraranum* (Miq.) C. DC.	Piperaceae
495	*Acalypha villosa* Jacq.	Euphorbiaceae
496	*Ocotea* sp.	Lauraceae
497	*Iresine diffusa* Willd.	Amaranthaceae
498	*Catasetum barbatum* (Lindley) Lindley, vel aff.	Orchidaceae
499	*Euterpe* sp.	Arecaceae
	no locality, no date	
499-A	*Bactris monticola* Barb. Rodr.	Arecaceae
	no locality, no date	
501	*Cecropia sciadophylla* C. Martius	Moraceae
502	*Ipomoea alba* L.	Convolvulaceae
503	*Casearia sylvestris* Sw. var. *sylvestris*	Flacourtiaceae
504	*Mikania vitifolia* DC.	Asteraceae
	no locality, no date	
505	*Mikania leiostachya* Benth.	Asteraceae
	no locality, no date	
506	*Palicourea nitidella* (Muell. Arg.) Standley	Rubiaceae
507	*Guazuma ulmifolia* Lam.	Sterculiaceae
?509	*Clidemia rubra* (Aublet) C. Martius	Melastomataceae
	no locality, no date	
?509	*Apinagia richardiana* (Tul.) van Royen	Podostemaceae
	El Motin (lower ranges), 13 Sep. 1951	
509-A	*Miconia matthaei* Naud.	Melastomataceae
510	*Mikania psilostachya* DC.	Asteraceae
	no locality, no date	
511	*Cecropia latiloba* Miq.	Moraceae
512	*Stromanthe* aff. *jacquinii* (Roemer & Schultes) Kennedy & Nicolson	Marantaceae
513	*Aphelandra deppeana* Schldl. & Cham.	Acanthaceae
516	*Micropholis egensis* (A. DC.) Pierre	Sapotaceae
517		Araceae
518	*Aniseia martinicensis* (Jacq.) Choisy	Convolvulaceae

519	*Bauhinia glabra* Jacq.	Caesalpiniaceae
520	*Nectandra cuspidata* Nees	Lauraceae
521	*Psychotria calviflora* Steyerm.	Rubiaceae
523	*Thoracocarpus bissectus* (Vell. Conc.) Harling	Cyclanthaceae
524	*Campyloneurum phyllitidis* (L.) C. Presl	Polypodiaceae
525	*Ocotea glomerata* (Nees) Mez	Lauraceae
?527-bis	*Pithecellobium divaricatum* Benth.	Mimosaceae
?527-bis	*Inga nobilis* Willd.	Mimosaceae
528	*Bactris corossilla* Karsten	Arecaceae
	no locality, no date	
529	*Monstera obliqua* Miq.	Araceae
530	*Sarcoglottis* sp.?	Orchidaceae
531	*Maxillaria camaridii* Reichb.f.	Orchidaceae
533	*Stanhopea grandiflora* (Ludd.) Lindley	Orchidaceae
534	*Catasetum barbatum* (Lindley) Lindley	Orchidaceae
536	*Quiina parvifolia* Pulle	Quiinaceae
538	*Aechmea setigera* C. Martius ex Schultes f.	Bromeliaceae
539	*Aechmea angustifolia* Poeppig & Endl.	Bromeliaceae
540-A	*Piper* sp.	Piperaceae
	no locality, no date	
541	*Coussapoa* sp.	Moraceae
542	*Psilotum nudum* (L.) Pal.	Psilotaceae
543	*Begonia humilis* Aiton	Begoniaceae

SALTO CODAZZI, 30 AUG. 1951; 02°15′N, 64°20′W; ca. 150 m elev.

543-A	*Begonia humilis* Aiton	Begoniaceae

ISLA DE LAS HORMIGAS, 30 AUG.; 02°15′N, 64°18′30″N

544	*Ficus paraensis* (Miq.) Miq.	Moraceae

PTO. ESPERANZA, 31 AUG.; 02°14′58″N, 64°16′44″W; 177 m elev.

546	*Rinorea pubiflora* (Benth.) Sprague & Sandw.	Violaceae

ISLA DEL ESFUERZO, 1–5 SEP. 1951; 02°15′N, 64°17′W

547	Possible mixed collection: *Guatteria schomburgkeana* C. Martius + *Anaxagorea dolichocarpa* Sprague & Sandw.	Annonaceae
548	*Thoracocarpus bissectus* (Vell. Conc.) Harling Isla de Hormigas, 7 Sep. 1951	Cyclanthaceae
550	*Cissus sicyoides* L.	Vitaceae
551	*Caraipa* sp.	Clusiaceae
552	*Dioscorea abysmophila* Maguire & Steyerm.	Dioscoreaceae
553	*Passiflora vespertilio* L.	Passifloraceae
554	*Sabicea velutina* Benth. subsp. *duidensis* Steyerm.	Rubiaceae
556	*Cissampelos pareira* L.	Menispermaceae
557	*Calyptranthes fasciculata* O. Berg	Myrtaceae
558	*Turnera odorata* Urban	Turneraceae
559	*Physalis pubescens* L.	Solanaceae
560	*Apteria aphylla* (Nutt.) Barnhart ex Small	Burmanniaceae
561	*Monotagma plurispicatum* (Koern.) Schum.	Marantaceae
562	*Schefflera morototoni* (Aublet) Maguire, Steyerm. & Frodin	Araliaceae
563	*Epiphyllum phyllanthus* (L.) Haw.	Cactaceae

LOS TIESTOS, 7–10 SEP. 1951; 02°13′N, 64°10′W

564	*Aechmea rubiginosa* Mez	Bromeliaceae
565	*Croton boultonianus* Croizat	Euphorbiaceae
566	*Erythrochiton brasiliensis* Nees & C. Martius	Rutaceae
568	*Microgramma megalophylla* (Desv.) Sota	Polypodiaceae
569	*Hylaeanthe* sp.	Marantaceae
570	*Abuta grandifolia* (C. Martius) Sandw.	Menispermaceae
?571	*Metaxya rostrata* (HBK) Presl	Metaxyaceae
?571	*Microgramma tecta* (Kaulf.) Alston	Polypodiaceae
572	*Apeiba schomburgkii* Szyszyl.	Tiliaceae
573	*Philodendron scandens* C. Koch	Araceae

574	*Orthomene schomburgkii* (Miers) Barneby & Krukoff	Menispermaceae
575	*Monstera adansonii* Schott var. *laniata* (Schott) Madison	Araceae
576	*Adiantum serratodentatum* Willd.	Adiantaceae
578	*Scaphyglottis sickii* Pabst	Orchidaceae
580	*Peperomia serpens* (Sw.) Loudon	Piperaceae
580-A	*Piper hispidum* Sw. f. *hispidum*	Piperaceae
	no locality, no date	
581	*Phthirusa pyrifolia* (HBK) Eichler	Loranthaceae

EL MOTIN, 12–14 SEP. 1951; 02°13′N, 64°10′W

582	*Ficus guianensis* Desv.	Moraceae
583	*Eugenia* sp.	Myrtaceae
584	*Socratea exorrhiza* (C. Martius) Wendl.	Arecaceae
	no locality, no date	
585	*Oncidium nanum* Lindley	Orchidaceae
586	*Gustavia poeppigiana* O. Berg	Lecythidaceae
	La Esmeralda, 16 July 1951	
586-A	*Eschweilera pedicellata* (Rich.) S. Mori	Lecythidaceae
587	*Calycolpus goetheanus* (DC.) O. Berg	Myrtaceae
588	*Psychotria* aff. *platypoda* A. DC.	Rubiaceae
589	*Randia venezuelensis* Steyerm.	Rubiaceae
590	*Matelea stenopetala* Sandw.	Asclepiadaceae
591	*Apinagia longifolia* (Tul.) van Royen	Podostemaceae
592	*Esenbeckia pilocarpoides* Kunth subsp. *pilocarpoides*	Rutaceae
592-A	*Esenbeckia pilocarpoides* Kunth subsp. *pilocarpoides*	Rutaceae
593	*Passiflora longiracemosa* Ducke	Passifloraceae
?594	*Psychotria racemosa* (Aublet) Raeusch.	Rubiaceae
?	*Morinda tenuiflora* (Benth.) Steyerm. var. *leiophylla* (Steyerm.) Steyerm.	Rubiaceae
595		Rubiaceae?
596	*Dieffenbachia seguine* (L.) Schott	Araceae
597	*Angostura trifoliata* (Willd.) T. Elias	Rutaceae
598	*Acalypha* cf. *macrostachya* Jacq.	Euphorbiaceae
599	*Eschweilera pedicellata* (Rich.) S. Mori	Lecythidaceae
600	*Eschweilera pedicellata* (Rich.) S. Mori	Lecythidaceae
600-A	*Eschweilera coriacea* (DC.) C. Martius ex O. Berg	Lecythidaceae
	no locality, no date	
601	*Oxandra* sp.	Annonaceae
603	*Vismia cayennensis* (Jacq.) Pers.	Clusiaceae
605	*Calliandra stipulacea* Benth.	Mimosaceae
605-bis	*Calliandra stipulacea* Benth.	Mimosaceae
606		Haemodoraceae
607	*Campyloneurum phyllitidis* (L.) C. Presl	Polypodiaceae
608	*Pouteria caimito* (Ruíz Lopez & Pavón) Radlk.	Sapotaceae
610	*Vanilla pompona* Schiede	Orchidaceae
611	cf. *Stromanthe jacquinii* (Roemer & Schultes) Kennedy & Nicolson	Marantaceae
612	*Piper francovilleanum* C. DC.	Piperaceae
613	*Calathea densa* (Koch) Regel	Marantaceae
614	*Mecardonia procumbens* (Miller) Small	Scrophulariaceae
	Salto Salas, 15 Sep. 1951	

RAUDAL BOBADILLA, 15–16 SEP. 1951; 02°13′N, 64°07′W; ca. 200 m. elev.

617	*Dioclea virgata* (Rich.) Amshoff var. *virgata*	Fabaceae
618	*Caladium bicolor* (Aiton) Vent.	Araceae
619	*Mabea* sp.	Euphorbiaceae
620	*Miconia* cf. *bubalina* (Don) Naud.	Melastomataceae
621	*Passiflora coccinea* Aublet	Passifloraceae
	Ugueto, 15 Sep. 1951	
622	*Brosimum guianense* (Aublet) H. E. Huber	Moraceae
623	*Rinorea* sp.	Violaceae
624	*Ouratea croizatii* Maguire & Steyerm.	Ochnaceae
625	*Jacaranda obtusifolia* subsp. *rhombifolia* (G. Mey) A. Gentry	Bignoniaceae
626	*Oldenlandia lancifolia* (Schumann) A. DC.	Rubiaceae
627	*Brassia bidens* Lindley	Orchidaceae
628	*Mabea occidentalis* Benth.	Euphorbiaceae
630	*Ocotea* sp.	Lauraceae

EL QUESO, 17 SEP. 1951

631	*Dichorisandra hexandra* (Aublet) Standley	Commelinaceae
633	*Guarea guidonia* (L.) Sleumer	Meliaceae
634	*Hylocereus* sp.	Cactaceae
635	*Microgramma reptans* (Cav.) A. R. Smith	Polypodiaceae
637	*Pithecellobium latifolium* Benth.	Mimosaceae
638	*Anthurium sinnuatum* Gleason	Araceae
639	*Chamissoa altissima* (Jacq.) HBK	Amaranthaceae

RAUDAL MONTSERRAT, 17 SEP. 1951; 02°08′N, 63°53′W

642	*Polypodium hygrometricum* Splitg.?	Polypodiaceae
643	*Tectaria incisa* Cav.	Aspleniaceae
644	*Triplophyllum funestrum* (Kunze) Holttum	Tectariaceae

RAUDAL BOBADILLA, 17–18 SEP. 1951; 02°13′N, 64°07′W

645	*Teliostachya cataractae* Nees	Acanthaceae
646	*Aphelandra deppeana* Schlecht. & Cham.	Acanthaceae
647	*Aphelandra* sp.	Acanthaceae
	Raudal Montserrat	
648	*Campylocentrum poeppigii* (Reichb.f.) Rolfe	Orchidaceae

RAUDAL MONTSERRAT, 19–20 SEP. 1951; 02°08′N, 63°53′W

649	*Guettarda divaricata* (Humb. & Bonpl. ex Roemer & Schultes) Standley	Rubiaceae
650	*Psychotria bracteocardia* (A. DC.) Muell. Arg.	Rubiaceae
651	*Asplenium claussenii* Hieron.?	Aspleniaceae
652	*Pityrogramma calomelanos* (L.) Link	Adiantaceae
653	*Trichilia* sp.	Meliaceae
654	*Sauvagesia erecta* L.	Ochnaceae
655	*Phytolacca rivinioides* Kunth & Bouché	Phytolaccaceae
656	*Paypayrola* sp.	Violaceae
657	*Epidendrum* (paniculatum group)	Orchidaceae
657-A	*Epidendrum secundum* Jacq.	Orchidaceae
659	*Hamelia patens* Jacq. var. *glabra* Oersted	Rubiaceae
660	*Mendoncia* sp.	Acanthaceae
661	*Stizophyllum riparium* (HBK) Sandw.	Bignoniaceae
	Los Tiestos, 9 Sep. 1951	
662	*Psychotria deflexa* A. DC. subsp. *campyloneura* (Muell. Arg.) Steyerm.	Rubiaceae
663	*Lindsaea lancea* (L.) Bedd. × *L. divaricata* Klotzsch?	Dennstaedtiaceae
664	*Duguetia* sp.	Annonaceae
666	*Cestrum strigilatum* Ruíz Lopez & Pavón	Solanaceae
667	*Pleurothallis* sp.	Orchidaceae
670	*Mendoncia sprucei* Lindau	Acanthaceae
671	*Palicourea calophylla* A. DC.	Rubiaceae
672	*Pouteria surumuensis* Baehni	Sapotaceae
673	*Nidema ottonis* Reichb. f.	Orchidaceae
674	*Pteris pungens* Willd.	Adiantaceae
674-bis	*Metaxya rostrata* (HBK) Presl	Metaxyaceae
675	*Adiantum petiolatum* Desv.	Adiantaceae
675-bis	*Lomariopsis japurensis* (C. Martius) J. Sm.	Aspleniaceae
676	*Bulbophyllum pachyrhachis* (A. Rich.) Griseb.	Orchidaceae
678-A	*Piper arboreum* Aublet var. *arboreum*	Piperaceae
	no locality, no date	
679	*Heteropsis tenuispadix* Bunting	Araceae
680	*Piper bartlingianum* (Miq.) C. DC.	Piperaceae
681	*Besleria laxiflora* Benth.	Gesneriaceae
682	*Psygmorchis pusilla* (L.) Dodson & Dressler	Orchidaceae
682-A	*Psygmorchis pusilla* (L.) Dodson & Dressler	Orchidaceae
682-B	*Psygmorchis pusilla* (L.) Dodson & Dressler	Orchidaceae
	La Mantequilla, 24 Sep. 1951	
682-C	*Pleurothallis* sp.	Orchidaceae
	La Mantequilla, 24 Sep. 1951	
683	*Scaphyglottis boliviense* (Rolfe) B. R. Adams, vel aff.	Orchidaceae
685	*Odontocarya* sp.	Menispermaceae

687	*Oxandra* sp.	Annonaceae
688	*Calyptranthes fasciculata* O. Berg	Myrtaceae
689		Myristicaceae
691	*Vittaria costata* Kunze	Adiantaceae
	Pica de la Mantequilla, 20 Sep. 1951	
692	*Hemicrepidospermum rhoifolium* (Benth.) Sw.	Burseraceae
694	*Adiantum dolosum* Kunze	Adiantaceae
695	*Blechnum occidentale* L.	Blechnaceae
696	*Corynostylis arborea* (L.) S. F. Blake	Violaceae
697	*Spathiphyllum canniifolium* (Dryander) Schott	Araceae

LA MANTEQUILLA, 21–23 SEP. 1951; 02°08′N, 63°52′W

698	*Batemannia colleyi* Lindley	Orchidaceae
699	*Vittaria costata* Kunze	Adiantaceae
700	*Selaginella umbrosa* Lem. ex Hieron.	Selaginellaceae
701	*Tectaria plantaginea* (Jacq.) Maxon var. *macrocarpa* (Fée) C. Morton	Aspleniaceae
702	*Aciotis indecora* (Bonpl.) Triana var. *macrophylla* Cogn.	Melastomataceae
	Raudal Montserrat, 21 Sep. 1951	
703	*Doryopteris sagittifolia* (Raddi) J. Sm.	Adiantaceae
	Raudal Montserrat, 21 Sep. 1951	
704	*Peristeria guttata* Knowls & Westc., vel aff.	Orchidaceae
705	*Trichomanes ekmanii* W. Boer	Hymenophyllaceae
706	*Diplazium grandifolium* (Sw.) Sw.	Aspleniaceae
707	*Campyloneurum angustifolium* (Sw.) Fée	Polypodiaceae
708	*Trichomanes collariatum* Bosch	Hymenophyllaceae
710	*Campyloneurum repens* (Aublet) C. Presl	Polypodiaceae
711	*Asplenium serratum* L.	Aspleniaceae
712	*Asplenium auritum* Sw., s.l.	Aspleniaceae
?713	*Asplenium cirrhatum* Rich. ex Willd.	Aspleniaceae
?713	*Perama galioides* (HBK) Poiret	Rubiaceae
	La Esmeralda, 14 July 1951	
714	*Diodia ocimifolia* (Willd.) Bremek.	Rubiaceae
715	*Masdevallia norae* Luer	Orchidaceae
716	*Pleopeltis percussa* (Cav.) Hook. & Grev.	Polypodiaceae
717	*Polypodium polypodioides* (L.) Watt. var. *burchellii* (Baker) Weath.	Polypodiaceae
718	*Mollinedia* sp.	Monimiaceae
718-A	*Mollinedia* sp.	Monimiaceae
	Salto Rojas, 25 Sep. 1951	
718-B	*Mollinedia* sp.	Monimiaceae
	no locality, no date	
719	*Hecistopteris pumila* (Sprengel) J. Sm.	Adiantaceae
720	*Campyloneurum phyllitidis* (L.) C. Presl	Polypodiaceae
721	*Antrophyum guayanense* Hieron.	Adiantaceae
722	*Renealmia monosperma* Miq.	Zingiberaceae
723	*Asplenium haplophyllum* Domin	Aspleniaceae
724	*Dichaea trinitensis* Gleason	Orchidaceae
725	*Campylocentrum micranthum* (Lindley) Rolfe	Orchidaceae
726	*Diplazium cristatum* (Desr.) Alston	Aspleniaceae
727	*Trema integerrima* (Beurling) Standley	Ulmaceae
728	*Tectaria trinitensis* Maxon	Aspleniaceae
729	*Pleopeltis percussa* (Cav.) Hook. & Grev.	Polypodiaceae
730	*Trichomanes ekmanii* W. Boer	Hymenophyllaceae
731	*Aspasia variegata* Lindley	Orchidaceae
732	*Microgramma persicariifolia* (Schrader) C. Presl.	Polypodiaceae
733	*Niphidium crassifolium* (L.) Lellinger	Polypodiaceae
733-bis	*Grammitis mollissima* (Fée) Proctor	Polypodiaceae
734	*Triplophyllum funestrum* (Kunze) Holttum	Tectariaceae
735	*Asplenium auritum* Sw., s.l.	Aspleniaceae

SALTO ROJAS, 25 SEP. 1951; 02°08′N, 63°50′W; ca. 300 m elev.

736	*Maranta humilis* Aublet	Marantaceae
?737	*Thelypteris* × *rolandii* (C. Chr.) R. Tryon	Thelypteridaceae
?737	*Drymonia coccinea* (Aublet) Wiehler	Gesneriaceae
738	*Ardisia guianensis* (Aublet) Mez	Myrsinaceae
740	*Virola elongata* (Benth.) Warb.	Myristicaceae
741	*Sciaphila purpurea* Benth.	Triuridaceae

742	*Loreya mespilioides* Miq.	Melastomataceae
743	*Souroubea dasystachya* Gilg & Werderman	Marcgraviaceae
744	*Pleurothallis* sp.	Orchidaceae
	no locality, no date	
745	*Miconia tomentosa* (Rich.) Don	Melastomataceae
746	*Pleurothallis* sp.	Orchidaceae
747	*Psychotria acuminata* Benth.	Rubiaceae
748	*Bauhinia ungulata* L.	Caesalpiniaceae
750	*Dieffenbachia duidae* (Steyerm.) Bunting	Araceae
751	*Nectandra globosa* (Aublet) Mez, s.l.	Lauraceae
753	*Sciaphila purpurea* Benth.	Triuridaceae
754	*Cheiloclinium serratum* (Cambess.) A. C. Smith	Hippocrateaceae
755	*Ludwigia foliobracteolata* (Munz) H. Hara	Onagraceae
755-A	*Ludwigia foliobracteolata* (Munz) H. Hara	Onagraceae
	no locality, no date	
755-B	*Ludwigia leptocarpa* (Nutt.) H. Hara	Onagraceae
	no locality, no date	
756	*Codonanthe calcarata* (Miq.) Hanst.	Gesneriaceae
757	*Cyathea pungens* (Willd.) Domin	Cyatheaceae
757-bis	*Thelypteris tristis* (Kunze) R. Tryon	Thelypteridaceae
758	*Urera baccifera* (L.) Gaudich.	Urticaceae
758-A	*Urera baccifera* (L.) Gaudich.	Urticaceae
	no locality, no date	

UGUETO, 29 SEP. 1951; 02°08′22″N, 63°48′47″W; 300 m elev.

762	*Clarisia* sp.	Moraceae
763	*Stelis* sp.	Orchidaceae
764	*Desmodium wydlerianum* Urban	Fabaceae
764-bis	*Metaxya rostrata* (HBK) Presl	Metaxyaceae
	Raudal Montserrat, 19 Sep. 1951	
765	*Diplazium cristatum* (Desr.) Alston	Aspleniaceae
767	*Thoracocarpus bissectus* (Vell. Conc.) Harling	Cyclanthaceae
	mixed with inflorescence of *Asplundia* sp.	
768	*Brosimum lactescens* (S. Moore) C. C. Berg	Moraceae
769	*Bixa orellana* L.	Bixaceae
770	*Dryopteris guianense* (Klotzsch) L. D. Gómez	Aspleniaceae
771	*Adiantum humile* Kunze	Adiantaceae
771-bis	*Trichomanes collariatum* Bosch, vel aff.	Hymenophyllaceae
?772	*Psychotria ulviformis* Steyerm.	Rubiaceae
	no locality, no date	
?772	*Miconia dispar* Benth.	Melastomataceae
773	*Miconia lateriflora* Cogn.	Melastomataceae
774	*Byttneria catalpifolia* Jacq. subsp. *catalpifolia*	Sterculiaceae
775	*Gurania trialata* Cogn.	Cucurbitaceae
776		Clusiaceae
777	*Pleurothallis* sp.	Orchidaceae
778	*Elaphoglossum flaccidum* (Fée) T. Moore	Aspleniaceae
780	*Psychotria racemosa* (Aublet) Raeusch.	Rubiaceae
782	*Cyclodium guianense* (Klotzsch) L. D. Gómez	Aspleniaceae
783	*Microgramma tecta* (Kaulf.) Alston	Polypodiaceae
784	*Nephrolepis biserrata* (Sw.) Schott	Davilliaceae
784-bis	*Asplenium claussenii* Hieron. vel. aff.	Aspleniaceae
785	*Brugmansia suaveolens* (Willd.) Bercht. & Presl	Solanaceae
787	*Peperomia serpens* (Sw.) Loudon	Piperaceae
788	*Adiantum terminatum* Kunze ex Miq.	Adiantaceae
789	*Paullinia bracteosa* Radlk.	Sapindaceae
790	*Tropaeolum fintelmanii* Wagener ex Schldl.	Tropaeolaceae
791	*Psychotria horizontalis* Sw. var. *glaucescens* (HBK) Steyerm.	Rubiaceae
792	*Morinda tenuiflora* (Benth.) Steyerm. var. *leiophylla* (Steyerm.) Steyerm.	Rubiaceae
793	*Bolbitis semipinnatifida* (Fée) Alston	Aspleniaceae
794	*Asplenium delitescens* (Maxon) L. D. Gómez	Aspleniaceae
795	*Polypodium decumanum* Willd.	Polypodiaceae
796	*Mendoncia cardonae* Leonard	Acanthaceae
797	*Hymenophyllum hirsutum* (L.) Sw.	Hymenophyllaceae
797-A	*Hymenophyllum polyanthos* (Sw.) Sw.	Hymenophyllaceae
797-B	*Hymenophyllum polyanthos* (Sw.) Sw.	Hymenophyllaceae

798	*Saccoloma elegans* Kaulf.	Dennstaedtiaceae
799	*Conceveiba guianensis* Aublet	Euphorbiaceae
800	*Bertiera guianensis* Aublet subsp. *guianensis* var. *guianensis*	Rubiaceae
801	*Guarea grandifolia* DC.	Meliaceae
803	*Dendropanax arboreum* (L.) Decne. & Planchon	Araliaceae
804	*Chamissoa altissima* (Jacq.) HBK	Amaranthaceae
805	*Adenocalymma impressum* (Rusby) Sandw.	Bignoniaceae
806	*Dicranoglossum desvauxii* (Klotzsch) Proctor	Polypodiaceae
808	*Adiantum terminatum* Kunze ex Miq.	Adiantaceae
809	*Bunchosia decussiflora* W. R. Anders.	Malpighiaceae
809-A	no locality, no date	Clusiaceae
810	*Apeiba aspera* Aublet	Tiliaceae
811	*Trichomanes diversifrons* (Bory) Mett. ex Sadeback	Hymenophyllaceae
811-bis	*Selaginella parkeri* (Hook. & Grev.) Spring	Selaginellaceae
812	*Psychotria poeppigiana* Muell. Arg. subsp. *barcellana* (Muell. Arg.) Steyerm.	Rubiaceae
813	*Posadaea sphaerocarpa* Cogn.	Cucurbitaceae
814	*Manettia reclinata* Mutis	Rubiaceae
814-A	*Psychotria ulviformis* Steyerm.	Rubiaceae
815	*Sagotia racemosa* Baillon	Euphorbiaceae
816	*Rinorea pubiflora* (Benth.) Sprague & Sandw.	Violaceae
817	*Lindackeria paludosa* (Benth.) Gilg	Flacourtiaceae
818	*Rinorea lindeniana* (Tul.) Kuntze	Violaceae
819	*Micropholis egensis* (A. DC.) Pierre	Sapotaceae
821	*Didymochlaena truncatula* (Sw.) J. Sm.	Aspleniaceae
822	*Dicranoglossum desvauxii* (Klotzsch) Proctor	Polypodiaceae
823	*Hylaeanthe* sp.	Marantaceae
824	*Trichomanes pinnatum* Hedwig	Hymenophyllaceae
825	*Ryania speciosa* Vahl. var. *bicolor* (A. DC.) Monach.	Flacourtiaceae
826	*Martiodendron excelsum* (Benth.) Gleason	Caesalpiniaceae
827	*Theobroma bicolor* Humb. & Bonpl.	Sterculiaceae

RAUDAL DEL QUESO, 17 OCT. 1951

828	*Inga sertulifera* DC.	Mimosaceae

UGUETO, 23 OCT. 1951

829	*Polypodium caceresii* Sodiro	Polypodiaceae

The following collections use the Croizat numbering series on the labels, but mention no localities or dates. It is believed that these are the collections of Pablo Anduze and Luis Carbonell from the Río Orinoco, above Ugueto. Ugueto was the furthest point that Croizat traveled on the expedition. The collections seem to have been arranged by family, but many were improperly identified and so do not follow the numerical sequence exactly.

830	*Ruellia rubra* Aublet	Acanthaceae
831	*Mendoncia cardonae* Leonard	Acanthaceae
832	*Chamissoa altissima* (Jacq.) HBK	Amaranthaceae
833	*Annona* sp.	Annonaceae
834	*Duguetia* sp.	Annonaceae
835	*Guatteria cardoniana* R. E. Fries	Annonaceae
836	Mixed collection: *Anaxagorea* sp. + Clusiaceae	Annonaceae + Clusiaceae
837	*Guatteria cardoniana* R. E. Fries	Annonaceae
?838	*Annona* sp.	Annonaceae
?838		Clusiaceae
839	*Guatteria recurvisepala* R. E. Fries	Annonaceae
?840	*Ferdinandusa goudotiana* Schumann var. *eciliata* Steyerm.	Rubiaceae
?840	*Cymbopetalum brasiliense* (Vell. Conc.) Benth.	Annonaceae
841	*Tabernaemontana heterophylla* Vahl	Apocynaceae
842	*Monstera obliqua* Miq.	Araceae
842-A	*Monstera dubia* (HBK) Engl.	Araceae
843	*Monstera lechleriana* Schott	Araceae
843-A	*Monstera obliqua* Miq.	Araceae
844	*Piper cernuum* Vell. Conc.?	Piperaceae
844-A	*Monstera dubia* (HBK) Engl.	Araceae
845	*Heteropsis tenuispadix* Bunting	Araceae

846	*Dieffenbachia seguine* (Jacq.) Schott	Araceae
847	*Monstera obliqua* Miq.	Araceae
848	*Monstera dubia* (HBK) Engl.	Araceae
849	*Philodendron scandens* C. Koch & Sello	Araceae
850	*Heteropsis melinonii* (Engl.) A. Jonker & Jonker	Araceae
851		Araceae
852	*Philodendron maguirei* Bunting	Araceae
853	*Anthurium gracile* (Rudge) Schott	Araceae
854	*Monstera obliqua* Miq.	Araceae
855		Araceae
856	*Tabebuia pilosa* A. Gentry	Bignoniaceae
856-A	*Crescentia amazonica* Ducke	Bignoniaceae
856-B	*Paragonia pyramidata* (Rich.) Bureau	Bignoniaceae
856-C	*Cydista aequinoctialis* (L.) Miers	Bignoniaceae
857	*Bixa orellana* L.	Bixaceae
858	*Aechmea penduliflora* André	Bromeliaceae
859		Anacardiaceae
860		Burseraceae
863	Mixed collection: Hylaeanthe sp. + leaves of cf. *Calathea splendens* (Lem.) Regel	Marantaceae
864	*Melothria pendula* L.	Cucurbitaceae
866	*Sloanea guianensis* (Aublet) Benth.	Elaeocarpaceae
867	*Satyria panurensis* (Benth.) Benth. & Hook.f.	Ericaceae
867-A	*Thibaudia nutans* Mansf.	Ericaceae
867-B	*Agarista duckei* (Huber) Judd	Ericaceae
867-C	*Befaria sprucei* Meissner	Ericaceae
868	*Conceveiba guianensis* Aublet	Euphorbiaceae
868-G	*Conceveiba guianensis* Aublet	Euphorbiaceae
868-H	*Hieronima laxiflora* (Tul.) Muell. Arg.	Euphorbiaceae
868-I	*Hieronima oblonga* (Tul.) Muell. Arg.	Euphorbiaceae
869	*Maprounea guianensis* Aublet	Euphorbiaceae
869-F	*Alchornea* sp.	Euphorbiaceae
870	*Hieronima laxiflora* (Tul.) Muell. Arg.	Euphorbiaceae
870-E	*Acalypha villosa* Jacq.	Euphorbiaceae
871	*Aparisthmium cordatum* (A. Juss.) Baillon	Euphorbiaceae
871-D	*Mabea occidentalis* Benth.	Euphorbiaceae
872	*Alchornea* sp.	Euphorbiaceae
872-C	*Phyllanthus orbiculatus* Rich.	Euphorbiaceae
873	*Aparisthmium cordatum* (A. Juss.) Baillon	Euphorbiaceae
873-B	*Mabea* sp.	Euphorbiaceae
874	*Acalypha macrostachya* Jacq.	Euphorbiaceae
874-A	*Acalypha macrostachya* Jacq.	Euphorbiaceae
875	*Asplenium cirrhatum* Rich. ex Willd.	Aspleniaceae
876	*Pleopeltis percussa* (Cav.) Hook. & Grev.	Polypodiaceae
877	*Asplenium auritum* Sw.	Aspleniaceae
878	*Polypodium triseriale* Sw.	Polypodiaceae
879	*Polypodium triseriale* Sw.	Polypodiaceae
880	*Triplophyllum funestrum* (Kunze) Holttum	Tectariaceae
881	*Dicranoglossum desvauxii* (Klotzsch) Proctor	Polypodiaceae
882	*Anetium citrifolium* (L.) Splitg.	Adiantaceae
883	*Selaginella diffusa* (C. Presl) Spring	Selaginellaceae
884	*Cochlidium tepuiense* (A. C. Smith) L. E. Bishop	Polypodiaceae
885		Flacourtiaceae
886	*Casearia arborea* (Rich.) Urban	Flacourtiaceae
887		Flacourtiaceae
888	*Ryania speciosa* Vahl var. *bicolor* (A. DC.) Monach.	Flacourtiaceae
889	*Besleria* sp.	Gesneriaceae
900	*Caraipa tereticaulis* Tul. Of doubtful occurrence in Venezuela, det. K. Kubitzki	Clusiaceae
900-A		Clusiaceae
901	*Caraipa punctulata* Ducke	Clusiaceae
902		Clusiaceae
903		Clusiaceae
904		Clusiaceae
904-A	*Couepia guianensis* Aublet subsp. *guianensis*	Chrysobalanaceae
905	*Clusia* sp.	Clusiaceae

906		Clusiaceae
907		Clusiaceae
?908-B	*Caraipa punctulata* Ducke	Clusiaceae
?908-B	*Irlbachia alata* (Aublet) P. Maas subsp. *alata*	Gentianaceae
908-C	*Epistephium* sp.	Orchidaceae
?909		Clusiaceae
?909	*Hyptis mutabilis* (Rich.) Briq.	Lamiaceae
?910		Clusiaceae
?910	*Ocotea aciphylla* (Nees) Mez	Lauraceae
911	*Ocotea aciphylla* group, flowers diseased, probably *O. aciphylla* (Nees) Mez	Lauraceae
912	*Ocotea cernua* (Nees) Mez	Lauraceae
913	cf. *Nectandra cuspidata* Nees	Lauraceae
914	*Ocotea* sp.	Lauraceae
915	*Nectandra reticulata* (Ruíz Lopez & Pavon) Mez	Lauraceae
916	*Ocotea guianensis* Aublet	Lauraceae
917	*Rhodostemonodaphne kunthiana* (Nees) Rohwer	Lauraceae
918	*Persea croizatii* van der Werff	Lauraceae
919		Lauraceae
919-B	*Endlicheria gracilis* Kosterm.	Lauraceae
919-C	*Nectandra cuspidata* Nees	Lauraceae
919-D	*Aiouea guianensis* Aublet	Lauraceae
919-E	*Nectandra cuspidata* Nees	Lauraceae
921	*Senna silvestris* (Vell. Conc.) H. Irwin & Barneby	Caesalpiniaceae
923	*Senna multijuga* (Rich.) H. Irwin & Barneby	Caesalpiniaceae
924	*Phaseolus appendiculatus* Benth.	Fabaceae
?930	*Acacia polyphylla* DC.	Mimosaceae
?930	*Mucuna* sp.	Fabaceae
931	*Senna bacillaris* (L.f.) H. Irwin & Barneby	Caesalpiniaceae
933	*Mucuna urens* (L.) DC.	Fabaceae
934	*Inga pezizifera* Benth.	Mimosaceae
938	*Smilax* sp.	Liliaceae
939	*Centropogon cornutus* (L.) Druce	Campanulaceae
943	*Mascagnia macrodisca* (Triana & Pl.) Niedenzu	Malpighiaceae
944	*Bunchosia decussiflora* W. R. Anders.	Malpighiaceae
945	*Stigmaphyllon hypoleucum* Miq.	Malpighiaceae
946	*Bunchosia decussiflora* W. R. Anders.	Malpighiaceae
947	*Monotagma laxum* (Poeppig & Endl.) Schum.	Marantaceae
948-A	*Heliconia episcopalis* Vell. Conc.	Musaceae
948-B	*Renealmia alpinia* (Rottb.) P. Maas	Zingiberaceae
948-C		Marantaceae
948-D	*Renealmia aromatica* (Aublet) Griseb.	Zingiberaceae
948-E	*Renealmia aromatica* (Aublet) Griseb.	Zingiberaceae
948-F	*Costus arabicus* L.	Zingiberaceae
949	*Miconia* cf. *minutiflora* (Bonpl.) DC.	Melastomataceae
949-A	*Bellucia grossularioides* (L.) Triana	Melastomataceae
950	*Miconia* sp.?	Melastomataceae
950-A	*Miconia amplexans* (Crueg.) Cogn.	Melastomataceae
951	*Miconia spennerostachya* Naud.	Melastomataceae
	Surely from Peru or Bolivia, not Venezuela, det. Wurdack	
952	*Miconia centrodesma* Naud.	Melastomataceae
953	*Bellucia grossularioides* (L.) Triana	Melastomataceae
954	*Miconia dispar* Benth.	Melastomataceae
955	*Aciotis purpurascens* (Aublet) Triana	Melastomataceae
956	*Ficus maxima* P. Miller	Moraceae
957	*Cecropia membranacea* Trécul	Moraceae
958	*Ficus* sp.	Moraceae
959	*Coussapoa viridifolia* Cuatrec.	Moraceae
960	*Ficus eximia* Schott	Moraceae
961	*Coussapoa* sp.	Moraceae
962	*Pourouma melinonii* Benoist	Moraceae
963	*Ficus nymphaeifolia* P. Miller	Moraceae
964	*Brosimum guianense* (Aublet) H. E. Huber	Moraceae
968-A	*Iryanthera hostmanii* (Benth.) Warb.	Myristicaceae
968-B	*Virola sebifera* Aublet	Myristicaceae
969	*Osteophloeum platyspermum* (DC.) Warb.	Myristicaceae
970	*Osteophloeum platyspermum* (DC.) Warb.	Myristicaceae
971	*Cybianthus viridiflorus* A. C. Smith	Myrsinaceae

973	*Calycolpus goetheanus* (DC.) O. Berg	Myrtaceae
973-A	*Calyptranthes fasciculata* O. Berg	Myrtaceae
973-B	*Myrcia bracteata* (Rich.) DC.	Myrtaceae
973-C	*Myrcia dichasialis* McVaugh La Esmeralda, 10 July 1951	Myrtaceae
975	*Caularthron bicornutum* (Hook.) Raf.	Orchidaceae
975-A	Mixed collection: *Scaphyglottis* sp. + *Epidendrum strobiliferum* Reichb.f.	Orchidaceae
976	*Notylia* sp.	Orchidaceae
976-A	*Epidendrum strobiliferum* Reichb.f.	Orchidaceae
977	*Oncidium nanum* Lindley	Orchidaceae
977-A	*Brassia caudata* (L.) Lindley	Orchidaceae
978	*Orleanesia* sp.	Orchidaceae
978-A	*Brassia caudata* (L.) Lindley	Orchidaceae
979	*Brassia* sp.	Orchidaceae
979-A	*Dichaea brachypoda* Reichb.f.	Orchidaceae
980	*Maxillaria amazonica* Schltr.	Orchidaceae
981	*Sigmatostalix amazonica* Schltr.	Orchidaceae
982	*Oncidium* sp.	Orchidaceae
983	*Sobralia fragrans* Lindley	Orchidaceae
984	*Oncidium cebolleta* (Jacq.) Sw.	Orchidaceae
985	*Vanilla pompona* Schiede	Orchidaceae
986	*Orleanesia* sp.	Orchidaceae
987	*Scaphyglottis prolifera* Cogn., vel aff.	Orchidaceae
988	*Clowesia warscewiczii* (Reichb.f.) Dodson	Orchidaceae
989	*Dichaea pendula* (Aublet) Cogn., vel aff.	Orchidaceae
990	*Bollea hemixantha* Reichb. f.	Orchidaceae
991	*Epidendrum secundum* Jacq., vel aff.	Orchidaceae
992	*Epidendrum schomburgkii* Lindley	Orchidaceae
993	*Quekettia microscopica* Lindley	Orchidaceae
994	*Iriartella setigera* (C. Martius) Wendl.	Arecaceae
995	*Iriartella setigera* (C. Martius) Wendl.	Arecaceae
995-A	*Hyospathe elegans* C. Martius	Arecaceae
995-B	*Geonoma* sp.	Arecaceae
995-C	*Bactris corossilla* Karsten	Arecaceae
996	*Passiflora* cf. *maguirei* Killip	Passifloraceae
1000-A	*Piper cernuum* Vell. Conc.?	Piperaceae
1001	*Piper* sp.	Piperaceae
1001-A	*Piper* cf. *augustum* Rudge	Piperaceae
1006	*Piper* sp.	Piperaceae
1016	*Securidaca* sp.	Polygalaceae
1017	*Gouania* sp.	Rhamnaceae
1019	*Psychotria barbiflora* A. DC.	Rubiaceae
1020	*Palicourea guianensis* Aublet subsp. *occidentalis* Steyerm.	Rubiaceae
1021	*Palicourea guianensis* Aublet subsp. *occidentalis* Steyerm.	Rubiaceae
1022	*Psychotria tepuiensis* (Steyerm.) Steyerm.	Rubiaceae
1023	*Palicourea nitidella* (Muell. Arg.) Standley	Rubiaceae
1024	*Psychotria berteriana* A. DC. subsp. *luxuriana* (Rusby) Steyerm.	Rubiaceae
1025	*Palicourea nitidella* (Muell. Arg.) Standley	Rubiaceae
1026	*Rudgea woronowii* Standley	Rubiaceae
1027	*Psychotria barbiflora* A. DC.	Rubiaceae
1028	*Psychotria microbotrys* Ruíz Lopez ex Standley	Rubiaceae
1029	*Psychotria poeppigiana* Muell. Arg. subsp. *barcellana* (Muell. Arg.) Steyerm.	Rubiaceae
1030	*Ferdinandusa goudotiana* Schumann var. *eciliata* Steyerm.	Rubiaceae
1031	*Schradera polycephala* A. DC.	Rubiaceae
1032	*Psychotria alba* Ruíz Lopez & Pavón, new to Venezuela	Rubiaceae
1033	*Paullinia ingaefolia* Rich.	Sapindaceae
1035	*Paullinia ingaefolia* Rich.	Sapindaceae
1036		Sapotaceae
1037	*Chrysophyllum sanguinolentum* (Pierre) Baehni subsp. *balata* (Ducke) Penn.	Sapotaceae
1038		Burseraceae
1040		Anacardiaceae
1040-B		Burseraceae
1040-C	*Toulicia pulvinata* Radlk.	Sapindaceae
1040-D	*Cupania scrobiculata* Rich.	Sapindaceae
1040-E	*Paullinia leiocarpa* Griseb.	Sapindaceae

1042	*Virola sebifera* Aublet	Myristicaceae
1043		Myrsinaceae
1044	*Besleria* sp.	Gesneriaceae
1044-A	*Besleria laxiflora* Benth.	Gesneriaceae
1044-B	*Codonanthe crassifolia* (Focke) Morton	Gesneriaceae
1045	*Aechmea penduliflora* André	Bromeliaceae
1045-A	*Aechmea* cf. *chantinii* (Carrière) Baker	Bromeliaceae
1046	*Caraipa tereticaulis* Tul. Of doubtful occurrence in Venezuela, det. Kubitzki	Clusiaceae
1047	*Amphirrhox latifolia* C. Martius	Violaceae
1048		Clusiaceae
1049	*Pouteria? filipes* Eyma	Sapotaceae
1051	*Byttneria catalpifolia* Jacq. subsp. *catalpifolia*	Sterculiaceae
1052	*Tontelea ovalifolia* (Miers) A. C. Smith	Hippocrateaceae
1052-A	*Pouteria? filipes* Eyma	Sapotaceae
1052-B	*Anaxagorea dolichocarpa* Sprague & Sandw.	Annonaceae
1052-C	*Endlicheria* sp.	Lauraceae
1053	*Solanum rugosum* Dunal	Solanaceae
1054		Solanaceae
1055	*Solanum subinerme* Jacq.	Solanaceae
1059	*Freziera calophylla* Triana & Planchon	Theaceae
1060	*Schlegelia spruceana* Schumann	Bignoniaceae
1061	*Schlegelia spruceana* Schumann	Bignoniaceae
1062	*Rinorea pubiflora* (Benth.) Sprague & Sandw.	Violaceae
1063		Violaceae
1064		Burseraceae
1065-A	*Rinorea* sp.	Violaceae
1065-B	*Rinorea falcata* (C. Martius) Kuntze	Violaceae
1066	*Schradera polycephala* A. DC.	Rubiaceae
1067	*Palicourea nitidella* (Muell. Arg.) Standley (probably)	Rubiaceae
1068	*Palicourea nitidella* (Muell. Arg.) Standley	Rubiaceae
1069	*Tabernaemontana heterophylla* Vahl	Apocynaceae
1070	*Tabernaemontana heterophylla* Vahl	Apocynaceae

2. Family List

This list is arranged into two major groups: Pteridophytes and Angiosperms. Within the two groupings, the collections are arranged in alphabetical order by: family, genus, and species, followed by Croizat's collection number(s).

Pteridophytes

ADIANTACEAE

Adiantum cajennense Willd. ex Klotzsch	295
Adiantum dolosum Kunze	694
Adiantum humile Kunze	771
Adiantum latifolium Lam.	486
Adiantum petiolatum Desv.	675
Adiantum pulverulentum L.	482
Adiantum serratodentatum Willd.	576
Adiantum terminatum Kunze ex Miq.	788, 808
Anetium citrifolium (L.) Splitg.	882
Antrophyum guayanense Hieron.	721
Doryopteris sagittifolia (Raddi) J. Smith	703
Hecistopteris pumila (Sprengel) J. Smith	719
Pityrogramma calomelanos (L.) Link	490, 652
Pteris propinqua Agardh	277
Pteris pungens Willd.	674
Vittaria costata Kunze	691, 699

ASPLENIACEAE

Asplenium auritum Sw., s.l.	712, 735
Asplenium auritum Sw.	877
Asplenium cirrhatum Rich. ex Willd.	713, 875
Asplenium claussenii Hieron.?	275, 651, 784-bis
Asplenium delitescens (Maxon) L. D. Gómez	794
Asplenium haplophyllum Domin	723
Asplenium serratum L.	489, 711

BLECHNACEAE

Blechnum occidentale L.	695
Blechnum serrulatum Rich.	485

CYATHEACEAE

Cyathea pungens (Willd.) Domin	757

DAVALLIACEAE

Nephrolepis biserrata (Sw.) Schott	784

DENNSTAEDTIACEAE

Lindsaea lancea (L.) Bedd. × *L. divaricata* Klotzsch?	663
Lindsaea cf. *portoricensis* Desv.	164
Lindsaea stricta (Sw.) Dryander	123
Saccoloma elegans Kaulf.	798

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Bolbitis semipinnatifida (Fée) Alston — 793
Cyclodium guianense (Klotzsch) L. D. Gómez — 782
Cyclopeltis semicordata (Sw.) J. Smith — 315
Didymochlaena truncatula (Sw.) J. Smith — 821
Diplazium cristatum (Desr.) Alston — 726, 765
Diplazium grandifolium (Sw.) Sw. — 706
Dryopteris guianense (Klotzsch) L. D. Gómez — 770
Elaphoglossum flaccidum (Fée) T. Moore — 778
Lomariopsis japurensis (Mart.) J. Smith — 675-bis
Tectaria incisa Cav. — 347, 643
Tectaria plantaginea (Jacq.) Maxon var. *macrocarpa* (Fée) C. Morton — 701
Tectaria trinitensis Maxon — 728
Triplophyllum funestrum (Kunze) Holttum — 375, 405, 644, 734, 880

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Dicranopteris flexuosa (Schrader) L. Underw. — 434

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Cochlidium tepuiense (A. C. Smith) L. E. Bishop — 884
Grammitis mollissima (Fée) Proctor — 733-bis

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Hymenophyllum polyanthos (Sw.) Sw. — 797-A, 797-B
Trichomanes collariatum Bosch, vel aff. — 771-bis
Trichomanes collariatum Bosch — 708
Trichomanes diversifrons (Bory) Mett. ex Sadeback — 811
Trichomanes ekmanii W. Boer — 705, 730
Trichomanes pilosum Raddi — 165
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Lycopodiella camporum B. Øllg. & Wind. — 124
Lycopodiella caroliniana (L.) Pichi-Serm. var. *meridionalis* (Underw. & Lloyd) B. Øllg. & Wind. — 122

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Campyloneurum repens (Aublet) C. Presl — 710
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Microgramma megalophylla (Desv.) Sota — 358-bis, 568
Microgramma persicariifolia (Schrader) C. Presl — 285, 456, 732
Microgramma reptans (Cav.) A. R. Smith — 635
Microgramma tecta (Kaulf.) Alston — 121, 571, 783
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Polypodium bombycinum Maxon — 443, 468
Polypodium caceresii Sodiro — 829
Polypodium decumanum Willd. — 795
Polypodium hygrometricum Splitg.? — 642
Polypodium polypodioides (L.) Watt var. *burchellii* (Baker) Weath. — 717
Polypodium triseriale Sw. — 878, 879

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Selaginella flagellata Spring — 383
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Duguetia sp. 664, 834
Guatteria maypurensis Kunth 214
Guatteria cardoniana R. E. Fries 835, 837, 839
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Dieffenbachia duidae (Steyerm.) Bunting 750
Dieffenbachia seguine (Jacq.) Schott 596, 846
Heteropsis melinonii (Engl.) A. Jonker & Jonker 850
Heteropsis tenuispadix Bunting 679, 845
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Philodendron scandens C. Koch & Sello 573, 849
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Mikania leiostachya Benth. 505
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Cydista aequinoctialis (L.) Miers 300, 856-C
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Ocotea sp.	61, 224, 496, 630, 914
Ocotea aciphylla group, flowers diseased, probably *O. aciphylla* (Nees) Mez	911
Ocotea aciphylla (Nees) Mez	910
Ocotea cernua (Nees) Mez	912
Ocotea cymbarum HBK	27
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Calathea inocephala (Kuntze) Kennedy & Nicolson 74
Calathea propinqua (Poeppig & Endl.) Koen. 389
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Batemannia colleyi Lindley	698
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Brassavola martiana Lindley	163
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A PHYLOGENETIC REEVALUATION OF THE OLD WORLD SPECIES OF *FUCHSIA* (ONAGRACEAE)[1]

Jorge V. Crisci[2] *and Paul E. Berry*[3]

ABSTRACT

The four Old World species of *Fuchsia*—*F. cyrtandroides*, *F. excorticata*, *F. perscandens*, and *F. procumbens*—form a monophyletic group (sect. *Skinnera*) defined by blue pollen and the presence of flavones in all species. Data on foliar flavonoid compounds in the section were reanalyzed, and additional nonflavonoid characters were employed to make a phylogenetic reevaluation of the group, using the rest of the genus as the outgroup. Of 17 characters used, 7 were phylogenetically informative, resulting in two equally most parsimonious cladograms 23 steps long. Both have a consistency index of 0.75 when all noninformative characters are excluded. The two trees differ in the position of the Tahitian *F. cyrtandroides* and the New Zealand *F. procumbens*, each of which appears as the sister group of the other species in the respective cladograms. In both trees, *F. excorticata* and *F. perscandens* form a clade defined by constricted floral tubes. These results differ from a prior cladistic analysis of the section based primarily on flavonoids, which placed *F. cyrtandroides* unambiguously as the sister species of the rest of the section and grouped *F. procumbens* in a clade with *F. perscandens*.

Fuchsia is a genus of about 105 species found primarily in mountainous regions of the Neotropics. Four species comprising the distinctive sect. *Skinnera* are confined to the Old World, however, with three species in New Zealand and one on the island of Tahiti. This section is of considerable biogeographical interest for its marked disjunction from the American species and the presence of closely related taxa on distant islands in the South Pacific.

As part of a study of foliar flavonoid compounds in sect. *Skinnera*, Williams & Garnock-Jones (1986) presented a cladistic analysis of the group, based on their flavonoid results and several other characters. A single shortest tree resulted from their analysis, in which the Tahitian *F. cyrtandroides* is the sister species of a clade comprising all the New Zealand taxa, and the arborescent *F. excorticata* is the sister species of a clade formed by *F. procumbens* and *F. perscandens*, a creeping and a scandent species, respectively.

Independently, Averett et al. (1986) conducted a comprehensive survey of foliar flavonoids in the entire genus, including a greater number of samples in sect. *Skinnera* than in the earlier study by Williams & Garnock-Jones. Their study resulted in the detection of several compounds not previously found in the same taxa by Williams & Garnock-Jones (1986). This and new information derived from a revision of the section by Godley, Berry, and Smith (in prep.) prompted us to reassess the phylogenetic relationships within sect. *Skinnera*, using a reevaluation of flavonoid characters as well as a larger number of nonflavonoid characters.

MATERIALS AND METHODS

We recognize four species as terminal taxa in sect. *Skinnera* (Table 1). Three occur in New Zealand: the widespread tree fuchsia, *F. excorticata*, the lianoid *F. perscandens*, and the rare creeper, *F. procumbens*, which is restricted to the northern third of the North Island. Following Allan (1927, 1928), we treat *F.* ×*colensoi* as a series of interspecific hybrids between *F. excorticata* and *F. perscandens* and do not include it in our anal-

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TABLE 1. Taxa and geographical distributions in *Fuchsia* sect. *Skinnera*.

Taxa	Geographical distribution
F. cyrtandroides J. W. Moore	Tahiti (Society Islands)
F. excorticata (J. R. & G. Forster) Linnaeus f.	Throughout New Zealand, Chatham Islands, Stewart Island
F. perscandens Cockayne & Allan	New Zealand: throughout South Island, in southern half of North Island
F. procumbens R. Cunningham	New Zealand: restricted to northern third of North Island

ysis. The fourth species, *F. cyrtandroides*, grows as a small tree and is endemic to a few high peaks on Tahiti, in the Society Islands.

Character polarity was determined by the outgroup comparison method (Watrous & Wheeler, 1981; Maddison et al., 1984), collectively using the other sections of the genus as the outgroup since there is no single section that is a clear sister group. If sect. *Jimenezia* is used as the outgroup, based on the preliminary results of Sytsma & Smith's (1988) survey of chloroplast DNA restriction site mutations in *Fuchsia*, there are no differences in polarity assignment from using the other sections collectively.

The sources of the flavonoid data were Williams & Garnock-Jones (1986) and Averett et al. (1986). Where the two studies differed in the flavonoid profile of a particular species, the presence of a compound was employed in our analysis rather than its absence, since lack of detection can be due to presence in low concentrations, inadequate amounts of sample material, environmentally induced flavonoid changes, developmental differences, or natural intraspecific variation (Harborne, 1975; Bohm, 1987). Data on the sexual systems of the species were taken from Godley (1955, 1963, 1979). Field observations and analysis of preserved specimens were used to define the remaining floral and vegetative characters.

The data matrix used in this analysis is contained in Table 2. The data set was analyzed using the HENNIG86 phylogenetic package (version 1.5, Farris, 1988; Platnick, 1989), run on a Dell 200 computer applying the implicit enumeration option for calculating trees. We also used the successive weighting procedure (Farris, 1989), which calculates weights from the best fits to the most parsimonious trees and applies them in the weighting procedure until there are no changes in successively produced trees.

CHARACTER DEFINITION AND CODIFICATION

1. *Flavones:* the different biochemical pathway leading to the synthesis of flavones makes the presence of this class of compounds an important distinguishing character from taxa that have only flavonols (Gottlieb, 1975). The presence of flavones is generally an advanced trait (Harborne, 1975), but the secondary loss of such compounds can also constitute a third, highly advanced stage in flavonoid evolution (Gornall & Bohm, 1978; Averett & Raven, 1984). In view of this situation, we use the overall presence or absence of the flavone class in *Fuchsia* as a character, rather than treating each flavone compound individually. Presence of flavones is considered apomorphic in sect. *Skinnera*, since they are absent in sect. *Jimenezia* and in nearly all the other species of the genus. Absence = 0, presence = 1.

2. *Pollen:* blue pollen is very rare in the angiosperms and is found in *Fuchsia* only in sect. *Skinnera*. Anthers of *F. excorticata* are rich in three different anthocyanins (Crowden et al., 1977) and probably form a blue metallo-flavone-anthocyanin complex in living flowers (N. H. Fischer, pers. comm.). Cream-colored pollen = 0, blue pollen = 1.

3. *Ovule number:* all other sections of *Fuchsia* have fewer than 200 ovules per ovary, with ovules arranged in two rows per locule. This is also the case for *F. procumbens*, but the other three species in sect. *Skinnera* have more than twice the maximum number of ovules found in the other sections and have more than two rows of ovules per locule. < 200 ovules/ovary = 0, > 200 ovules/ovary = 1.

4. *Flavone sulphates:* these compounds are unusual among angiosperms (Harborne & Williams, 1982) and occur in *Fuchsia* only in sect. *Skinnera*. Absence = 0, presence = 1.

5. *Flavonol diglycosides:* flavonol monoglycosides were detected in all 80 taxa of the genus studied by Averett et al. (1986), whereas flavonol diglycosides occur in only a few taxa, including *F. excorticata* in sect. *Skinnera*. Absence = 0, presence = 1.

6. *Eriodictyol 7-glucuronide:* this uncommon flavanone has only been found within the genus in

TABLE 2. Data matrix for the taxa of *Fuchsia* sect. *Skinnera*; the other sections of *Fuchsia* are used as the outgroup. Character 7 is additive; characters 14 and 15 are nonadditive.

Taxa	Character																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
F. cyrtandroides	1	1	1	0	0	0	0	0	0	0	0	0	1	2	0	1	0
F. procumbens	1	1	0	1	0	0	2	1	1	1	1	0	0	0	2	0	1
F. perscandens	1	1	1	1	0	0	1	0	0	0	0	1	0	1	1	1	1
F. excorticata	1	1	1	1	1	1	1	0	0	0	0	1	0	2	0	1	1

F. excorticata (Williams et al., 1983). Absence = 0, presence = 1.

7. *Sexual system:* gynodioecy is derived from hermaphroditism in *F. procumbens* and *F. excorticata* by the presence of a dominant gene for male sterility. The addition of a linked gene dominant for female fertility in *F. procumbens* then leads to subdioecy. The other sections of *Fuchsia* are hermaphroditic or else have male sterility determined by a recessive gene (Breedlove et al., 1982). Hermaphroditic = 0, gynodioecious = 1, subdioecious = 2; additively (= sequentially) coded.

8. *Flower position:* hanging flowers characterize all but one other section of *Fuchsia*, with erect flowers in *F. procumbens* clearly derived. Hanging = 0, erect = 1.

9. *Petals:* petals are present in all but one other section of the genus. In sect. *Skinnera*, the petals are either much reduced or completely lacking in *F. procumbens*. Present = 0, lacking = 1.

10. *Stamens:* all species in the genus except *F. procumbens* have the stamens in two whorls of conspicuously different lengths. Distinct whorls = 0, stamens subequal = 1.

11. *Sepals:* sepals are spreading at anthesis in all but a few species of the other sections of the genus. In sect. *Skinnera*, *F. procumbens* is the only species with completely reflexed sepals doubling back against the floral tube. Spreading = 0, reflexed = 1.

12. *Floral tube:* floral tubes with little or no constriction is the prevalent condition in the outgroup. In sect. *Skinnera*, the tubes are either strongly constricted above the nectary and then abruptly widened above, or else cylindrical. Unconstricted = 0, strongly constricted = 1.

13. *Leaf texture:* membranous or subcoriaceous leaves occur in the rest of the genus, with *F. cyrtandroides* unique in its considerably thicker, crassate leaves. Membranous = 0, thick-crassate = 1.

14. *Leaf underside:* the presence of a silvery-white leaf underside is caused by the absence of chlorophyll in the spongy parenchyma of *F. excorticata* (Suckling, 1914) and is more specialized than the normal green leaf underside in the genus. *Fuchsia perscandens* has chlorophyll in the spongy parenchyma but also has a whitish underside. Green = 0, whitish = 1, silvery-white = 2; nonadditive (= unordered).

15. *Habit:* the outgroup is primarily shrubby and is here taken to include the small to medium-sized trees found in two species of sect. *Skinnera*. The unique creeping habit of *F. procumbens* and the unusual lianoid habit of *F. perscandens* are both specialized for the genus. Shrubby or tree = 0, lianoid = 1, procumbent creeper = 2; nonadditive.

16. *Flower color change:* flowers in three species of the section pass through an abrupt floral color change from green to red (Delph & Lively, 1985; Berry, unpublished). 0 = no distinct color phases, 1 = two distinct color phases.

17. *Leaf phyllotaxis:* leaves are initially opposite in all species of the section at the seedling stage, but in three species they become alternate soon thereafter. Opposite = 0, alternate = 1.

RESULTS

Two equally most parsimonious hypotheses were generated by our data matrix, designated here as cladogram A and cladogram B (Fig. 1). Both have 23 steps, with a consistency index of 0.75 after the noninformative characters were excluded. The successive weighting procedure did not discriminate either of the two trees, which differ only in the placement of *F. cyrtandroides* and *F. procumbens*. In cladogram A, *F. cyrtandroides* is the sister species of the three New Zealand species, while in cladogram B, *F. procumbens* is the sister species to *F. cyrtandroides*, *F. excorticata*, and *F. perscandens*. In both cladograms, *F. excorticata* and *F. perscandens* form a clade characterized by the presence of constricted floral tubes.

FIGURE 1. The two most parsimonious cladograms (length = 23; consistency index = 0.75 when noninformative characters are excluded) found from the analysis of the data matrix.—A. The topology in which *F. cyrtandroides* is the sister group of the New Zealand species.—B. The topology in which *F. procumbens* is the sister group of the rest of the section. Character state changes are superimposed on the cladograms; single lines = apomorphies, X = reversals.

Of the 17 characters used, 7 are informative in defining the phylogeny of the section. Only one of these remains as originally coded in both trees (#12, floral tube constriction), with the differences in the two trees determined by the evolution of the other six characters. In cladogram A, one extra step is required in each of three characters: 3 (ovule number), 14 (chlorophyll presence in spongy mesophyll), and 16 (floral color change), whereas in cladogram B the extra step occurs in characters 4 (flavone sulphates), 7 (sexual system), and 17 (leaf phyllotaxis). Characters 1 and 2 (flavones, blue pollen) are present in all members of the ingroup and define the section as a monophyletic group. Seven characters are autapomorphies (5, 6, 8, 9, 10, 11, and 13), with three additional autapomorphies in two multistate, nonadditive characters (14 and 15).

DISCUSSION

The main consequence of our reevaluation of flavonoid data in sect. *Skinnera* was a reduction in the number of flavonoid characters from seven (four informative) in Williams & Garnock-Jones (1986) to four in our analysis (only one of these informative). This was due to a more conservative choice of characters employed in our data matrix. We justify our use of flavonoid classes (instead of individual compounds) as being more congruent with current knowledge of flavonoid evolution, especially when the data are based on general surveys such as in *Fuchsia* (Gornall & Bohm, 1978; Richardson, 1983; Averett & Raven, 1984). Our matrix also reflects character state changes in some of the characters that were maintained in both studies, such as flavones in *F. cyrtandroides* and flavonol glycosides in *F. procumbens* and *F. perscandens*. These are "presences" of compounds that were not detected by Williams & Garnock-Jones (1986), but were found by Averett et al. (1986). Averett et al. (1986) examined 3–16 individuals per taxon in sect. *Skinnera* compared to 1–3 per taxon in Williams & Garnock-Jones (1986), which supports the use of larger sample sizes in

flavonoid surveys to more reliably detect the presence of compounds.

Our results differ considerably from the previous cladistic analysis of Williams & Garnock-Jones (1986), whose single shortest cladogram is shown in Figure 2. In their tree, *F. perscandens* forms a terminal clade with *F. procumbens*, whereas our results place *F. perscandens* in a terminal clade with *F. excorticata* (Fig. 1). Williams & Garnock-Jones used two flavonoid characters, presence of apigenin and loss of flavonols, as apomorphies defining their *perscandens-procumbens* clade, but the study by Averett et al. (1986) showed that both kinds of compounds are in fact found in all members of the section. Their third apomorphy for this clade, lianoid habit, is inappropriate, since it is unlikely that the creeping, barely woody character of *F. procumbens* is homologous with the woody, scandent habit of *F. perscandens*. The only character that defines our *perscandens-excorticata* clade is the strongly constricted floral tube, and this is probably associated with pollination by honeyeater birds (Meliphagidae) in these two species (Thomson, 1927; Delph & Lively, 1985). Bird pollination, on the other hand, is not known to occur in *F. procumbens*.

The other main difference in our cladistic analysis from that of Williams & Garnock-Jones is the ambiguous resolution of the sister species to the rest of the section (*F. cyrtandroides* or *F. procumbens*). With the Tahitian *F. cyrtandroides* as the sister species, our first hypothesis requires that *F. procumbens* (a) reverted back to a low ovule number, (b) regained chlorophyll in the spongy mesophyll (green leaf undersides), and (c) lost the derived floral color change. With *F. procumbens* as the sister species, *F. cyrtandroides* is required to have (a) lost flavone sulphates, (b) lost male sterility, and (c) reverted back to opposite leaves. This situation indicates that there must be extensive homoplasy in the section, but it is not yet evident from our results in which set of the above characters this has occurred.

The large number of autapomorphies in *F. procumbens* underscores how differentiated this species is from the rest of the section, yet does not help us determine if those characters are the result of a fundamental divergence or are a secondary development related to an unusual pollination syndrome or habitat type, for example. Because *F. procumbens* is now so rare in nature and its natural pollinators may have gone extinct, its pollination system remains unknown. The species is distinctive in *Fuchsia*, however, in occupying a seashore habitat, and it is restricted to the northern part of the

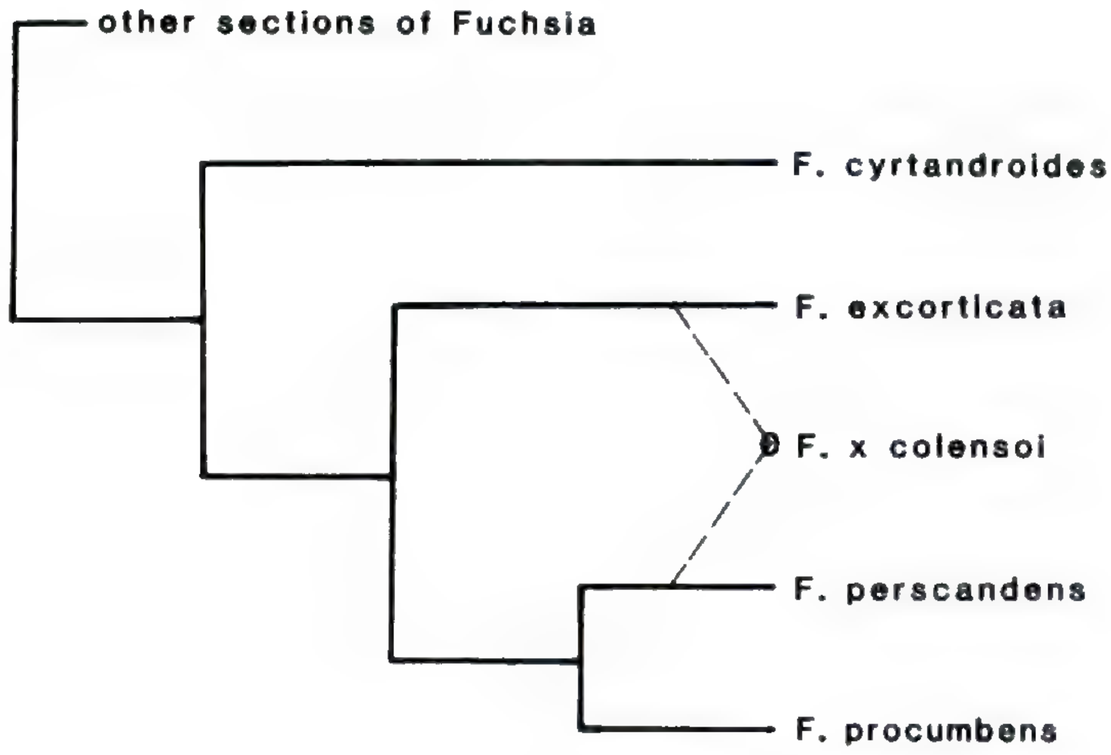

FIGURE 2. The single most parsimonious cladogram obtained by Williams & Garnock-Jones (1986); this differs from our hypotheses mainly in the position of *F. procumbens*.

North Island, an endemic-rich area of New Zealand (Craw, 1988).

Fuchsia's disjunct distribution between the New World and New Zealand and Tahiti has stimulated several hypotheses about its origin. Croizat, who opposed arguments of chance long-distance dispersal in *Fuchsia* and other groups, first considered the presence of the genus on Tahiti as an ancient one that exemplified the "trans-Pacific" track joining southeastern Brazil, south-central Chile, and the southwest Pacific (Croizat, 1962, p. 547). Later, Raven (1972, 1979a) suggested that *Fuchsia* reached New Zealand by trans-Pacific long-distance dispersal from South America, first to New Zealand by the mid-Miocene (to account for the fossil pollen of *Fuchsia* dated from that time; see Couper, 1960), then secondarily to Tahiti. More recently, Berry (1982) proposed an older, more direct connection from South America to New Zealand via Antarctica, with subsequent dispersal to Tahiti. This was based on older, Oligocene fossil records of *Fuchsia* from New Zealand (Mildenhall, 1980) and a newer understanding of the opportunities for direct migration across Antarctica until the Miocene (Raven, 1979b).

Most explanations for the presence of *Fuchsia* sect. *Skinnera* on Tahiti have been based on hypotheses of recent, probably bird-mediated dispersal from New Zealand (Carlquist, 1967, 1974; Fleming, 1976; Godley, 1979; Raven, 1979a; Berry, 1982). This view is based on the isolated oceanic position of Tahiti, its volcanic origin and recent age (less than two million years old; Dymond, 1975), and the fleshy fruit and small seeds of *F. cyrtandroides*. As a result of their cladistic analysis showing *F. cyrtandroides* to be the sister species of the rest of the section, Williams & Garnock-Jones (1986) dissented with this view, suggesting that *F.*

cyrtandroides was derived instead from the common ancestor of the section before the events that produced the different species in New Zealand. Although our results do not allow us to support one of these hypotheses, phylogenetic studies in other groups of organisms with similar distributions could help clarify the biogeographical relationships within *Fuchsia* sect. *Skinnera*. Our results do indicate, however, that we should place more emphasis on the possibility that *F. procumbens* is the sister species of the rest of the section, in which case its large suite of autapomorphies may reflect a long history of divergence from the rest of the group.

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PHYLOGENETIC IMPLICATIONS OF RIBOSOMAL DNA RESTRICTION SITE VARIATION IN THE PLANT FAMILY ONAGRACEAE[1]

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ABSTRACT

Phylogenetic relationships in the family Onagraceae were assessed using ribosomal DNA restriction site mapping. Sixty-five restriction sites were detected among 11 species of Onagraceae (one each of *Circaea*, *Fuchsia*, *Hauya*, *Oenothera*, and *Ludwigia*, and six species of *Epilobium*) using 20 restriction enzymes. Phylogenetic analysis of the data was performed using both Wagner and Dollo parsimony, and the resulting monophyletic groups were tested by the bootstrap method. The trees were rooted by using *Ludwigia* as a functional outgroup. Phenetic approaches (cluster analysis and principal coordinate analysis) were also applied to the data as a complement to the cladistic analysis. Wagner parsimony analysis generated four equally parsimonious trees (53 steps, consistency index 0.76), and Dollo parsimony analysis generated six equally parsimonious trees (59 steps, consistency index 0.67). In all trees the six species of *Epilobium* form a monophyletic group. Independent data on Onagraceae (morphological, cytological, anatomical, chemosystematic, and molecular) strongly support one of the six phylogenetic hypotheses generated by Dollo parsimony analysis, in which *Circaea*, *Fuchsia*, and *Hauya* form one branch with *Circaea* the sister group to *Fuchsia-Hauya*, and *Oenothera* and *Epilobium* form the other branch. Cluster analysis and principal component analysis do not agree with the phylogenetic analyses mainly in the position of *Epilobium*, suggesting the possibility of different rates of evolutionary change in different lines of the family.

Onagraceae are a well-defined family of flowering plants, consisting of seven tribes, 16 genera, and approximately 652 species of worldwide distribution (Raven, 1979, 1988). The family is unambiguously included in the order Myrtales (Dahlgren & Thorne, 1984; Johnson & Briggs, 1984), sharing with all members of the order a number of traits, including a distinctive set of eight embryological characters (Tobe & Raven, 1983). Within the order, Onagraceae are highly distinctive in the following features: (1) a characteristic four-nucleate embryo sac (Tobe & Raven, 1983); (2) the presence of abundant raphides in the vegetative cells (Metcalfe & Chalk, 1950; Carlquist, 1961, 1975); (3) the presence of septa dividing the sporogenous tissue (Tobe & Raven, 1986); (4) "paracrystalline beaded" pollen ektexine (Skvarla et al., 1975, 1976); and (5) viscin threads or ektexinous strands on the proximal pollen wall (Skvarla et al., 1978; Patel et al., 1984). Each of these features is a synapomorphy within Myrtales, and the combination of them strongly supports the naturalness of Onagraceae.

The family has been studied in close biosystematic detail, and modern taxonomic revisions are available or in preparation for all species. Leaf,

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TABLE 1. Tribes and genera of Onagraceae, with estimated numbers of species and geographical distributions of each (Raven, 1988).

	Estimated number of species	Geographical distribution
I. Jussiaeeae		
1. *Ludwigia*	82	Pantropical, best represented in South America; 3 sections with 21 species in temperate North America, 2 monotypic sections in temperate Asia; 7 species endemic to Africa, 1 to tropical Asia, and 2 endemics common; total of 25 species in Old World, 12 endemic.
II. Fuchsieae		
2. *Fuchsia*	105	Andean South America, with 12 species endemic in Mexico and Central America, 2 on Hispaniola, 8 in coastal Brazil, 1 in Tahiti, and 3 in New Zealand.
III. Circaeeae		
3. *Circaea*	7	North temperate forests and bordering alpine areas, 5 species endemic to Asia and all 7 found there.
IV. Lopezieae		
4. *Lopezia*	22	Mostly Mexican, 1 south to Guatemala and a second south to Panama.
V. Hauyeae		
5. *Hauya*	2	Mexico to Costa Rica.
VI. Onagreae		
6. *Gongylocarpus*	2	1 endemic to 2 islands off west coast of Baja California, 1 widespread in Mexico and Guatemala, but not common.
7. *Gayophytum*	9	Western North America, 1 endemic to temperate western South America and 1 common to both.
8. *Xylonagra*	1	Central Baja California.
9. *Camissonia*	61	Western North America, 1 endemic to temperate western South America.
10. *Calylophus*	6	Central US south to central Mexico.
11. *Gaura*	21	Southwestern and central US east to Atlantic coast and south to Mexico and Guatemala; centers in Texas.
12. *Oenothera*	123	70 North American, 49 South American, plus 4 common to both, 1 of European origin; far more diverse in North America, especially in west and in Mexico.
13. *Stenosiphon*	1	Great Plains of central US.
14. *Clarkia*	44	Western North America, all but 1 in California; 1 endemic to temperate western South America.
VII. Epilobieae		
15. *Epilobium*	162	Cosmopolitan at high altitudes and latitudes; 77 species in Eurasia (9 common to North America, 6 common to Africa), 46 in Australasia (all endemic), 35 in North America (26 endemic), 12 in South America (10 endemic), 10 in Africa (4 endemic).
16. *Boisduvalia*	6	Western North America, 1 in western temperate South America, 1 common to both continents.

wood, and floral anatomy have been studied in detail; chromosome numbers are known for most taxa; and breeding systems and pollinators, flavonoids, palynology, and embryology all have been investigated for most of the family. Because of this, Onagraceae are clearly the best-known plant family of their size from many points of view.

One surprising conclusion from these studies has been the distinctiveness of most genera of the family from one another; five of the seven tribes are monogeneric, and another includes two genera (Table 1). Pollen of Onagraceae has been recognized in the fossil record from the Maestrichtian Age (73–65 MYA) at the end of the Cretaceous Period

TABLE 2. Taxa analyzed, acronyms, and collection data. All vouchers deposited at MO unless otherwise noted. Abbreviation: MBG = Missouri Botanical Garden.

Acronym	Taxon	Collection data
CIR	*Circaea cordata* Royle	Cultivated MBG, *Hoch 1904*; seed from USSR, Vladivostok, *P. Raven in 1975.*
Ebi	*Epilobium billardierianum* Sér.	Cultivated MBG, *Hoch M3248*; seed from NEW ZEALAND, S. Island, Banks Peninsula, *Wilson & Sykes in 1984.*
Eci	*E. ciliatum* Raf.	Cultivated MBG, *Hoch M3187*; seed from USA, California, Marin Co., *M. Sharp in 1967.*
Ehi	*E. hirsutum* L.	Cultivated MBG, *Hoch M3259*; seed from INDIA, Ganderbal, *G. Dar in 1983.*
Eme	*E. melanocaulon* Hook.	A. Cultivated MBG, *Hoch M3356*; seed from NEW ZEALAND, S. Island, Flock Hill, *D.S.I.R. pop. X.* B. Cultivated MBG, *Hoch M3360*; seed from NEW ZEALAND, S. Island, Dry Creek, *D.S.I.R. pop. 11.* C. Cultivated MBG, *Hoch M3361*; seed from NEW ZEALAND, S. Island, Dry Creek, *D.S.I.R. pop. 12.*
Epa	*E. pallidiflorum* Sol. ex A. Cunn.	Cultivated MBG, *Hoch M3292*; seed from NEW ZEALAND, N. Island, *Gardner 4191.*
Ero	*E. royleanum* Hausskn.	Cultivated MBG, *Hoch M3258*; seed from INDIA, Sind Valley, *G. Dar 8664.*
FUC	*Fuchsia ×triphylla* L.	Cultivated MBG, *Hoch 1903*; from *Fuchsia* 'Gartenmeister', Longwood Garden, Pennsylvania 80/019!
HAU	*Hauya heydeana* Donn. Smith	Cultivated MBG, *Hoch M1499*; seed from MEXICO, Chiapas, *Breedlove 42080* (CAS).
LUD	*Ludwigia peploides* (HBK) Raven	USA, Missouri, St. Louis City, Forest Park, *Hoch 1900.*
OEN	*Oenothera biennis* L.	USA, Illinois, Calhoun Co., *Hoch & Hoch 1901.*

(Drugg, 1967; Pares Regali et al., 1974a, b), indicating that the very distinctive genera in the family may represent evolutionary lines that diverged in the remote past and subsequently have evolved separately (Raven, 1988). Because the genera are so well differentiated for the most part, phylogenetic reconstruction may prove to be particularly difficult.

A major phylogenetic hypothesis within the family is that *Ludwigia* is the sister group of all other Onagraceae. This was first suggested by Eyde (1977, 1979, 1981), based on the presence in *Ludwigia* alone of central vascular bundles in the ovary; massive, highly ovuliferous placentas; archaic nectary position; and 4+ merous perianths. Eyde's hypothesis is supported by data from chemosystematics (Averett & Raven, 1984) and cytology (Kurabayashi et al., 1962; Raven & Tai, 1979; Raven, 1988). Also, in a study of the 40 N-terminal amino acid residues of the small subunit of ribulose bisphosphate carboxylase, Martin & Dowd (1986) found that *Ludwigia* has a conventional terminal sequence common to most other plants, whereas the other ten species of Onagraceae examined share a highly distinctive sequence, accounting for at least three nucleotide differences. Despite the large amount of information available for the family, few other unambiguous hypotheses of relationships among the tribes and genera have been possible.

In view of the lack of resolution of the evolutionary relationships within Onagraceae based on the large base of morphological and chemosystematic evidence, the family may be an ideal group on which to use molecular methods to elucidate phylogeny. Results of these techniques will also contribute to the continuing debate within systematics regarding the best methods and the best type of data with which to reconstruct phylogenetic histories (Patterson, 1987).

Gottlieb and associates have utilized evidence derived directly or indirectly from changes in protein and DNA sequences to approach phylogenetic questions in Onagraceae. However, their work has focused primarily on relationships within *Clarkia* (Gottlieb, 1982; Sytsma & Gottlieb, 1986a, b) or *Fuchsia* (Sytsma & Smith, 1988), rather than between genera or tribes.

The conservative organization and evolution of ribosomal DNA (Hillis, 1987) make this molecule

well suited for comparative systematic investigations. Previous studies have clearly demonstrated the potential of rDNA for resolving evolutionary relationships because (1) it is mid to highly repetitive; (2) the rDNA repeat length is within a range that can be examined by restriction-fragment analysis; and (3) rDNA contains both slowly evolving regions (the 18S, 5.8S, and 28S ribosomal genes) and more rapidly evolving regions (the transcribed and nontranscribed spacers), so that information from various levels of evolutionary history can be recovered (Appels & Dvorák, 1982). Few phylogenetic studies using restriction map analyses of rDNA have been reported in the literature, and these are mostly confined to groups of closely related organisms (Sytsma & Schaal, 1985; Hillis & Davis, 1986).

Here we present a restriction-site analysis of rDNA as applied to questions of phylogenetic relationships among genera of the family Onagraceae, applying cladistic methods to analyze the restriction site variation. Some recent studies of this type of variation have applied a phenetic approach (Ovenden et al., 1987; Schaeffer et al., 1987; Yonekawa et al., 1988), and we have applied such approaches to our data as a complement to the cladistic analyses.

Two specific questions are addressed in this investigation: (1) What phylogenetic relationships can be deduced from the restriction-site data? and (2) Are they congruent with our present knowledge of Onagraceae?

Materials and Methods

TERMINAL TAXA

Eleven species of Onagraceae were analyzed; acronyms for these species, collection data, and geographical distributions are listed in Table 2. The taxa represent six of the seven tribes of Onagraceae (cf. Table 1); only Lopezieae were not available for this study. The six species of *Epilobium* included were chosen to allow assessment of the utility of the rDNA approach at the infrageneric level. We included three species of Australasian *Epilobium* (*Ebi*, *Eme*, *Epa*), a group thought to be closely related and recently evolved (Raven & Raven, 1976); a species from South Asia, *E. royleanum* (*Ero*), which is morphologically similar to the Australasian group and from a region thought to be the source area of that group; and two more distantly related species from Asia (*Ehi*) and North America (*Eci*) with no close affinities to the other species (Seavey & Raven, 1977, 1978). One population was sampled for each species except *E. melanocaulon*, for which three populations were examined to test for infraspecific site variation.

MOLECULAR TECHNIQUES

Total DNA was isolated from 10–50 grams of frozen leaves, stems, and immature inflorescences according to a previously published procedure (Zimmer et al., 1981); for members of the Onagraceae, most plant extractions required the use of antioxidants in the grinding buffer. Restriction endonuclease digestions, agarose gel electrophoresis, filter hybridizations, and autoradiography were performed as described in other studies of plant ribosomal gene organization (Sytsma & Schaal, 1985; Doyle & Beachy, 1985; Zimmer et al., 1988).

For production of rDNA maps, nitrocellulose filters with DNA fragments from single or double digests were successively probed with nick-translated DNA from the plasmids pXBr1, pGmr3, and pGmr1, which contained 5%, 50%, and 100% of a complete soybean repeat unit, respectively (Jupe et al., 1988; Zimmer et al., 1988). DNA fragments containing ribosomal-specific sequences were sized with a nonlinear regression analysis computer program (Learn & Schaal, 1987). Standard markers used included phage lambda DNA digested with EcoR I, Hind III, Sma I, or combinations thereof, and *Zea mays* rDNA fragments generated with BamH I. From the fragment sizes, and the positional information gained from the successive hybridization experiments, it was possible to generate and align the physical maps of restriction endonuclease cleavage sites for the Onagraceae ribosomal genes in the same manner described for other plant species (references cited above). A total of 65 restriction sites for 20 commercially available enzymes were mapped in the rDNA repeat units of all 11 species.

PHYLOGENETIC ANALYSIS

The restriction site data were analyzed using two different parsimony methods of phylogenetic analysis: Wagner and Dollo parsimony. The preferred tree with Wagner parsimony (Kluge & Farris, 1969; Farris, 1970) is the one of minimal length in a Manhattan metric (Farris, 1972, 1981), with no "a priori" restriction on the nature of permissible character state changes, i.e., with equal probability of parallel site losses and parallel site gains. In Dollo parsimony (Le Quesne, 1974; Farris, 1977), each character (restriction site) is assumed to have arisen only once on the tree; the preferred tree is the one that minimizes the number of subsequent

losses. Thus parallel site gains and loss-regains are strictly prohibited.

The bootstrap sampling method (Efron, 1979; Felsenstein, 1985) was used to place confidence intervals on monophyletic groups. This technique samples from the character set at random and provides the number of times that each partition of OTUs occurred. One hundred replicate samples were performed using Wagner and Dollo parsimony, and a majority-rule consensus tree was constructed (see review of consensus techniques in Smith & Phipps, 1984). The confidence intervals for each monophyletic group found in the consensus tree are given in percentages in the "consensus figures." The consensus tree of the bootstrap method does not necessarily have the same topology as the shortest tree(s) generated by Wagner or Dollo parsimony in the original analysis. This is a limitation of the consensus techniques (Miyamoto, 1985) as used in the construction of general cladograms and classification, but it is not necessarily problematic when used in association with the bootstrap method to reveal which clades are stable, unstable, or ambiguous.

The direction of evolutionary change (character-state polarization) of restriction sites was determined by outgroup comparison (Hennig, 1966; Watrous & Wheeler, 1981; Humphries & Funk, 1984). Sites present in both ingroup and outgroup are considered symplesiomorphic; sites present or absent in only part of the ingroup are considered synapomorphic. Whereas the best choice for outgroups would be other families of the order Myrtales (Dahlgren & Thorne, 1984), no data on rDNA restriction site variation are available for those groups. We performed the analysis using a functional outgroup for Onagraceae. The functional outgroup method formalized recently by Watrous & Wheeler (1981) works as follows: if some reliable criterion can be used for dividing the taxa into two or more groups, then these groups can be used as the outgroups of one another. The technique of "functional outgroup" can be applied effectively to Onagraceae because there is strong evidence from floral anatomy (Eyde, 1977, 1979, 1981) and molecular studies (Averett & Raven, 1984; Martin & Dowd, 1986) that *Ludwigia* (Jussiaeeae) represents a branch distinct from the rest of the family (Raven, 1979, 1988). Therefore we have used *Ludwigia* as a functional outgroup to polarize the restriction site data.

PHENETIC ANALYSIS

Cluster analysis and principal coordinate analysis, an ordination technique, were performed on the data. A Manhattan distance coefficient (Sneath & Sokal, 1973) between each pair of the 11 OTUs was calculated for the cluster analysis. The resulting OTU × OTU distance matrix was used to calculate a phenogram using the UPGMA clustering procedure (Romesburg, 1984). The cophenetic correlation coefficient was computed as a measurement of distortion (Sokal & Rohlf, 1962). Principal coordinate analysis (Gower, 1966) was performed on the OTU × OTU Manhattan distance matrix calculated in the cluster analysis procedure, and the first three factors were extracted. To examine the efficiency of the method, the Euclidean distance (Sneath & Sokal, 1973) between all pairs of OTUs in factor space was calculated using the eigenvector matrix, and the resulting OTU × OTU distance matrix was compared with the original distance matrix using the cophenetic correlation coefficient.

The computational work was performed on an IBM-AT microcomputer. Wagner and Dollo parsimony analyses were performed using PAUP (version 3.0, Swofford, 1988) with the branch and bound algorithm (Hendy & Penny, 1982). The bootstrap analysis was performed using PHYLIP (version 3.0; Felsenstein, 1985); the global option was used to find the shortest tree. Cluster analysis and principal coordinate analysis were performed using NTSYS-pc (version 1.22, Rohlf, 1987).

The Dollo program of the PAUP package assumes that the ancestor has all states 0. This assumption will rarely if ever be true with restriction site data, since any outgroup usually has a number of restriction sites present. In considering *Ludwigia* as the functional outgroup, we found that it did not have the fewest restriction sites among Onagraceae. In order to guarantee that *Ludwigia* would remain cladistically outside the functional ingroup, we had to force the monophyly of the remaining Onagraceae using the "CONSTRAINTS" option of PAUP. PHYLIP does not have a comparable option, so for the bootstrap runs we included an imaginary character that has 0 for *Ludwigia* and 1 for all the other OTUs. This imaginary character is then weighted 10 times. Although the new character brings 10 extra steps to the tree, these have been subtracted out of the total when reporting the results.

RESULTS

PATTERN OF RDNA REPEAT UNIT VARIATION

The rDNA repeat units from 11 species of Onagraceae were analyzed with 20 restriction endonucleases that for the most part cleave at six-base

TABLE 3. Ribosomal DNA restriction site mutations used in phylogenetic and phenetic analyses of 11 species of Onagraceae using 20 enzymes. Acronyms and voucher information for all species are listed in Table 2. Map positions (refer to Fig. 1) were derived primarily from *OEN*. Characters were scored as follows: 0 = site absence; 1 = site presence; ? = equivocal; — = no sample (? and — scores were treated as missing data in the analyses).

Site	Map position	*LUD*	*OEN*	*FUC*	*CIR*	*HAU*	*Eci*	*Epa*	*Ebi*	*Ero*	*Ehi*	*Eme*
1. Xba I	157	1	1	1	1	1	1	1	1	1	1	1
2. BamH I	576	1	1	1	1	1	1	1	1	1	1	1
3. Sac I	1363	1	1	1	1	1	1	1	1	1	1	1
4. Bgl I	1422	1	1	1	1	1	1	1	1	1	1	1
5. Sma I	1537	1	0	0	0	0	1	1	1	1	1	1
6. Tth I	1555	1	1	1	1	1	1	1	1	1	1	1
7. EcoR I	1572	1	1	1	1	1	1	1	1	1	1	1
8. BamH I	1629	0	0	?	0	0	0	0	0	0	0	0
9. Xmn I	1819	0	0	1	1	1	0	0	0	0	0	0
10. Sph I	1893	0	0	0	1	0	0	0	0	0	0	0
11. Bcl I	2011	0	0	0	0	0	1	1	1	1	1	1
12. EcoR V	2159	1	1	1	1	1	1	1	1	1	1	1
13. Sac I	2376	1	1	1	1	1	1	1	1	1	1	1
14. Tth I	2841	1	1	1	1	1	1	1	1	1	1	1
15. Sph I	3201	1	1	1	1	1	1	1	1	1	1	1
16. BamH I	3222	1	1	1	1	1	1	1	1	1	1	1
17. Xho I	3227	0	0	0	0	0	1	1	1	1	1	1
18. Sac I	3762	1	1	1	1	1	1	1	1	1	1	1
19. Stu I	3707	0	1	0	0	0	1	1	1	1	1	1
20. Sma I	3795	1	0	0	0	0	0	0	0	0	0	0
21. Bgl I	3798	1	1	1	1	1	0	0	0	0	0	0
22. Bgl II	3932	1	1	1	1	1	1	1	1	1	1	1
23. BamH I	4202	1	1	1	1	1	1	1	1	1	1	1
24. Xmn I	4232	1	1	1	1	1	1	1	1	1	1	1
25. Xho I	4245	0	0	0	0	0	1	1	1	1	1	1
26. Sma I	4359	1	0	0	0	0	0	0	0	0	0	0
27. Xmn I	4662	1	1	1	1	1	1	1	1	1	1	1
28. Tth III	4929	1	1	1	1	1	1	1	1	1	1	1
29. Sac I	5121	1	1	1	1	1	1	1	1	1	1	1
30. EcoR I	5373	1	1	1	1	1	1	1	1	1	1	1
31. Sph I	5445	1	1	1	1	1	1	1	1	1	1	1
32. Tth III	5487	1	1	1	1	1	1	1	1	1	1	1
33. Sac I	5578	0	0	0	0	0	1	1	1	1	1	1
34. Stu I	5742	0	0	0	0	0	0	1	0	0	0	0
35. Xmn I	5885	1	1	1	1	1	1	1	1	1	1	1
36. Xba I	5908	0	1	0	0	1	0	0	0	0	0	0
37. EcoR V	5993	0	0	0	0	0	1	1	1	1	1	1
38. Sph I	6083	0	0	0	0	0	1	0	0	1	1	0
39. Bcl I	6112	0	0	0	0	0	0	1	1	1	0	0
40. Hind III	6115	0	1	1	0	1	0	0	0	0	0	0
41. Stu I	6116	1	0	0	1	0	0	0	0	0	0	0
42. Sac I	6120	1	1	0	1	0	0	0	0	0	0	0
43. Nde I	6376	0	0	0	0	0	1	1	1	1	1	1
44. Tth I	6555	0	0	0	0	0	0	1	1	1	0	1
45. Xmn I	6726	0	0	0	0	0	1	0	0	1	0	0
46. EcoR I	6729	1	0	0	0	0	0	0	0	0	0	0
47. Sac I	6994	0	0	0	0	0	0	0	0	1	0	0
48. EcoR V	7358	1	0	0	0	0	0	0	0	0	0	0
49. Bcl I	7888	0	0	0	0	0	1	1	1	1	1	1
50. EcoR V	8069	0	0	0	0	0	1	1	1	1	1	1
51. Tth I	8184	0	0	0	0	0	1	1	1	1	1	1
52. BamH I	−1825	1	1	0	1	0	0	0	0	0	0	0

TABLE 3. Continued.

Site	Map position	*LUD*	*OEN*	*FUC*	*CIR*	*HAU*	*Eci*	*Epa*	*Ebi*	*Ero*	*Ehi*	*Eme*
53. BstE I	−1749	0	0	0	1	1	0	0	0	0	0	0
54. Stu I	−1702	1	0	0	1	0	0	0	0	0	0	0
55. Bgl I	−1174	1	0	1	0	1	0	0	0	0	0	0
56. Nde I	−1096	0	0	1	0	0	0	0	0	0	0	0
57. Bgl II	−902	0	0	1	0	0	0	0	0	0	0	0
58. BstE I	−665	1	0	1	1	0	0	0	0	0	0	0
59. Xho I	−500	—	0	1	0	0	0	0	0	0	0	0
60. BstE I	−299	1	0	1	0	0	0	0	0	0	0	0
61. Sca I	−212	0	0	—	1	1	0	0	0	0	0	0
62. Sph I	−176	1	1	1	1	1	0	0	0	0	0	0
63. Tth III	−50	0	1	1	1	1	0	0	0	0	0	0
64. Nde I	48	1	1	1	1	1	1	1	1	1	1	1
65. Xmn I	101	1	1	1	1	1	1	1	1	1	1	1

recognition sites. Sixty-five sites were mapped in the rDNAs of each species (Table 3; Fig. 1). Thirty-four of these 65 sites were in regions coding for the large, mature cytoplasmic ribosomal RNAs (positions 1–8, 14–37, and 64–65). Another five positions (9–13) occur in the internal transcribed spacer (ITS). All but one of the cleavage sites that were invariant (24/25) occurred in these transcribed portions of the ribosomal repeat unit. This pattern is similar to that observed with many other groups of higher plant rDNA repeat units (Sytsma & Schaal, 1985; Zimmer et al., 1988).

Extensive variation also was found for the length of inserts in the nontranscribed portion of the intergenic spacer region of the rDNAs (Table 4; Fig. 1). Although this variation was not phylogenetically informative, and therefore not used in any of the phylogenetic analyses reported here, there was some indication from the restriction site data that species sharing common inserts are closely related.

There were no restriction site differences found among the three population samples of *Epilobium melanocaulon*, and in Table 3 only one entry is recorded for this taxon. However, there were minor differences in repeat lengths among the samples (Table 4), indicating the presence of some infraspecific variation.

The basic data matrix consists of 65 restriction sites scored for each of 11 OTUs (Table 3). Only 34 of these mutations are phylogenetically informative, i.e., shared by two or more OTUs, 25 are constant among the 11 OTUs, and 6 are autapomorphies (i.e., unique mutations). The Wagner parsimony analysis resulted in four equally parsimonious trees (Fig. 2.I A–D) requiring a total of 53 steps, with a consistency index of 0.76 (Kluge & Farris, 1969). The calculation of the consistency index includes autapomorphies. When there was ambiguity in reconstructing the sequence of changes (Swofford & Maddison, 1987), gain-loss and parallel loss sequences were preferred over parallel gain and loss-regain sequences (Templeton, 1983a, b). The different kinds of homoplasious changes in the four trees are shown in Table 5.

In the four trees, with *Ludwigia* as outgroup, *Circaea* is the sister group of the rest of the family, and the six species of *Epilobium* form a monophyletic group. Inside *Epilobium* there are two hypotheses of relationships: (1) *Eci* and *Ehi* are a monophyletic group and the rest of the species are another monophyletic group; the latter has *Eme* as a sister species of the trichotomy *Epa-Ebi-Ero* (Fig. 2A, C); and (2) similar to the first, except *Ero* forms a monophyletic group with *Eci* and has *Ehi* as its sister group (Fig. 2B, D).

Aside from *Epilobium* there are also two hypotheses: (1) *Oenothera* is the sister group of *Fuchsia* and *Hauya*, the latter forming a sister group to *Epilobium*; and (2) *Fuchsia* is the sister group of *Hauya*, *Oenothera*, and *Epilobium*, with *Oenothera* as the sister group of *Epilobium*.

The majority-rule consensus tree constructed from 100 bootstrap samples (Fig. 2.II) shows that the six species of *Epilobium* form a highly significant (100%) monophyletic group. Within *Epilobium*, two groups occur with 50% or more frequency: *Ero-Eci* (50%) and *Ebi-Epa* (52%). The other two groups inside *Epilobium* have confidence intervals of less than 50%: *Ero-Eci-Ehi* (46%) and *Ebi-Epa-Eme* (27%). The group formed by the species of *Epilobium* plus *Oenothera* has a 39% confidence level, whereas *Fuchsia* and *Hauya* form

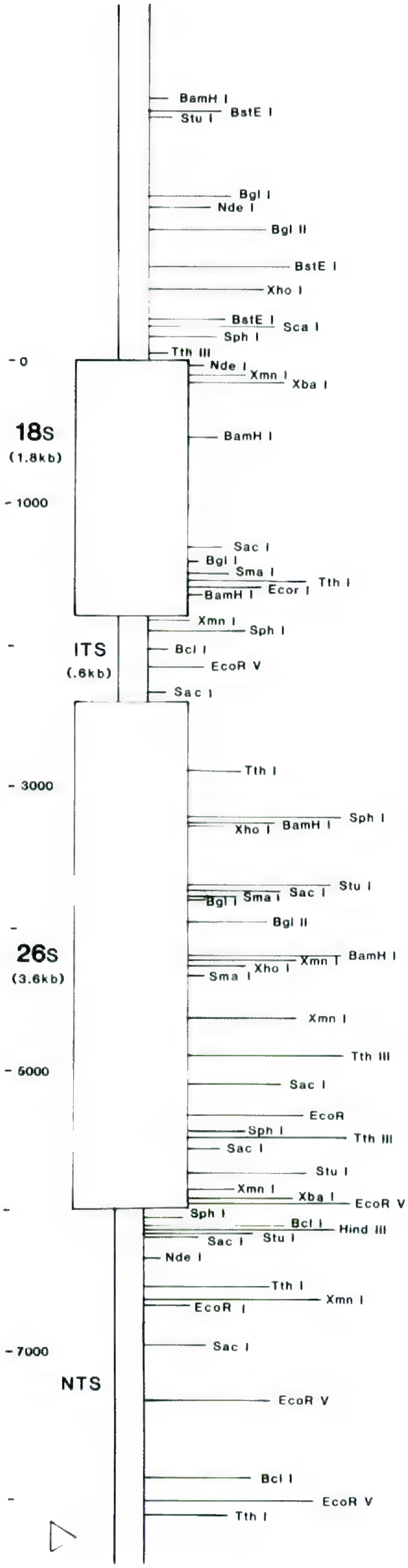

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FIGURE 1. Map of the Onagraceae ribosomal DNA repeat unit showing the location of 65 restriction sites mapped by 20 commercially available endonucleases. Map positions were derived primarily from *OEN*. Map includes 18S and 28S genes, internal transcribed spacer (ITS), and nontranscribed spacer (NTS). The triangle in the NTS indicates the approximate location of length mutations (Table 4). Region length and scale in kilobases (kb).

TABLE 4. Major repeat-unit lengths (kb) in rDNA of selected taxa of Onagraceae.

Taxon	Repeat units
LUD	6.9, 8.6, 10.6, 11.5
OEN	10.0, 13.0
FUC	9.3
CIR	9.2
HAU	7.7, 11.4, 12.6, 16.5
Eci	9.8, 10.6
Epa	8.8
Ebi	8.0
Ero	8.2, 8.6
Ehi	9.5, 10.4, 11.0, 11.5, 14.7
Eme A	8.1, 8.3
Eme B	8.3
Eme C	8.1, 8.3

a monophyletic group with a 46% confidence level. All of the OTUs beyond *Circaea* and *Ludwigia* form a monophyletic group with a 54% confidence level.

The Dollo parsimony analysis resulted in six equally parsimonious trees (Fig. 3) requiring a total of 59 steps, with a consistency index of 0.67. In this case, all homoplasious site changes are parallel losses or gain/losses. The six species of *Epilobium* form a monophyletic group in all trees. In three of the trees (A, C, E), there are four subgroups in *Epilobium* that are also monophyletic: ((((*Eme-Ebi-Epa*)*Ero*)*Eci*)*Ehi*), with (*Eme-Ebi-Epa*) as a trichotomy. In the other three trees (B, D, F), two monophyletic subgroups ((*Eci-Ehi*)*Ero*) form a trichotomy with *Ebi* and *Epa*, with *Eme* as outgroup to the other five species. *Oenothera* is the sister group of *Epilobium* in all trees. In four of the six trees (Fig. 3C–F), *Circaea* is the sister group of the remaining OTUs (excluding *Ludwigia*), and in the other two trees (Fig. 3A–B), *Circaea* forms a monophyletic group with *Fuchsia* and *Hauya*. *Fuchsia* and *Hauya* form a monophyletic group in four of the trees (Fig. 3A–B, E–F), but in the other two (Fig. 3C–D) *Fuchsia* is the sister group of the group formed by *Hauya*, *Oenothera*, and *Epilobium*.

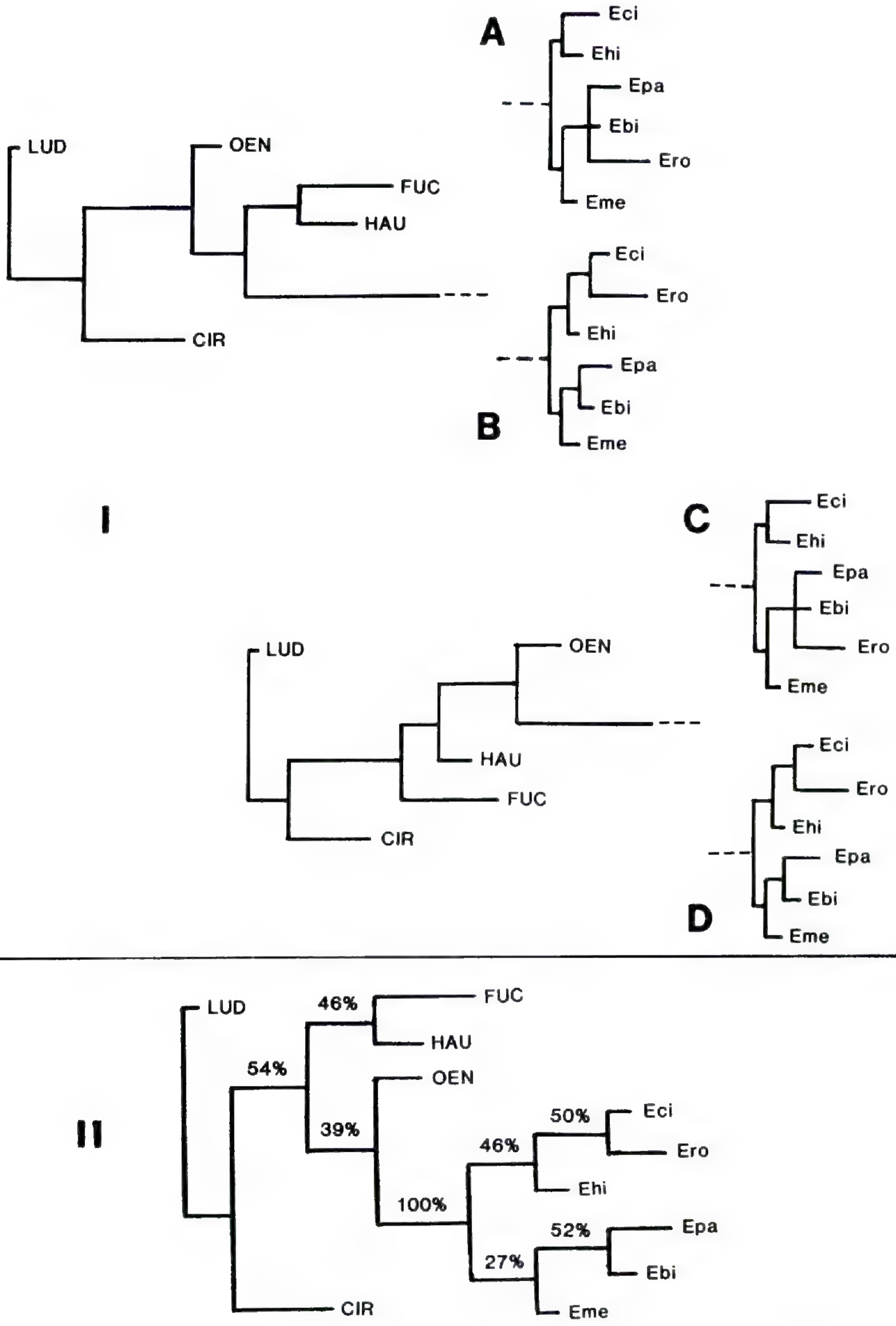

FIGURE 2. Wagner parsimony analysis for 11 species of Onagraceae, using *Ludwigia* as functional outgroup and based on 65 rDNA restriction site mutations. I. A–D, four alternative most parsimonious trees; length = 53, consistency index = 0.76. II. Majority-rule consensus tree constructed from 100 bootstrap samples. The percentages indicate the number of times that monophyletic group occurred in the bootstrap samples.

The majority-rule consensus tree constructed from 100 bootstrap samples is shown in Figure 4. The monophyletic group formed by the six species of *Epilobium* is highly significant (100%). Within *Epilobium* none of the four groups occurred with greater than 50% frequency. All the species of *Epilobium* and *Oenothera* form a monophyletic group 47% of the time. *Fuchsia* and *Hauya* form a monophyletic group 40% of the time, and *Circaea* joins them 30% of the time.

PHENETIC ANALYSIS OF RESTRICTION SITES

The basic data matrix (Table 3) of 11 OTU × 65 characters was analyzed by cluster analysis and by principal coordinate analysis.

1. *Cluster analysis.* Figure 5A presents the results of the cluster analysis using the UPGMA procedure. The phenogram has a high cophenetic correlation coefficient of 0.97. This indicates that the phenogram presents an accurate representation

TABLE 5. Homoplasious changes in four trees produced by Wagner parsimony analysis using *Ludwigia* as the functional outgroup, run with the ACCTRAN option of PAUP; numbers in parentheses derive from the DELTRAN option, which favors convergent gain over gain-loss; refer to Figure 2.

	Gain-loss	Loss-gain	Convergent gain	Convergent loss
Trees A–B	3 (1)	4 (4)	6 (8)	0 (0)
Trees C–D	5 (3)	4 (3)	3 (5)	1 (2)

of the original distance matrix. There are two well-defined and distant phenetic clusters: the six species of *Epilobium*, and the remaining OTUs. Inside the *Epilobium* cluster there are also two well-defined phenetic subgroups: *Eci-Ehi* and *Epa-Eme-Ebi*. *Ero* is an isolated OTU intermediate between the two *Epilobium* subgroups. *Ludwigia* is an isolated OTU in the other cluster. *Oenothera* and *Hauya* are grouped together, with *Fuchsia* and *Circaea* progressively less closely related to them.

2. *Principal coordinate analysis.* The results of the ordination method are shown in Figure 5B. The percentages of variation explained by each of the three factors are: I = 83.71%, II = 10.04%, and III = 4.39%. The total variation explained by this model is 98.14%, with a high correlation coefficient (0.99). These results therefore present an accurate representation of the original distance matrix. The principal coordinate analysis results in three basic, phenetically significant groups: (1) the six species of *Epilobium*; (2) *Oenothera*, *Fuchsia*, *Hauya*, and *Circaea*; and (3) *Ludwigia*. The six species of *Epilobium* form a closely related group, with *Ero* in a relatively isolated position, two groups of two OTUs each (*Eci-Ebi* and *Ehi-Eme*), and *Epa* in an intermediate position between *Ero* and *Eci-Ebi*. Within the group formed by *Oenothera*, *Hauya*, *Fuchsia*, and *Circaea*, the genera are much less close to each other than are the six species of *Epilobium* to each other. *Fuchsia* is relatively isolated in this group. Factor I is a good discriminator of *Epilobium* from the rest of the family; factor II is a good discriminator of *Ludwigia* from the rest of the family; and factor III is a good discriminator of *Fuchsia* from the rest of the family.

DISCUSSION

Restriction site data on the ribosomal DNA of Onagraceae provide valuable new information on the evolution of a diverse group of genera. Because rDNA contains both highly conserved coding regions and variable spacer regions, phylogenetically informative sites are found both within *Epilobium*, where many of the species are closely related (Raven & Raven, 1976), and between distantly related genera within the family.

PHYLOGENETIC ANALYSES

Trees A and B (Fig. 2.I) derived by Wagner analysis have *Oenothera* anomalously as a sister group to *Fuchsia*, *Hauya*, and *Epilobium*, in conflict with other trees and other phylogenetic information. In particular, *Oenothera* and *Epilobium* share several synapomorphies, including lobed stigmas, absence of stipules, and presence of interxylary phloem (Carlquist, 1975), none of which are shared with *Fuchsia* and *Hauya*. *Oenothera* also has very specialized chromosome number and structure compared with FUC-HAU (Kurabayashi et al., 1962; Raven, 1979, 1988).

In addition, trees A and B have more convergent site gains than do trees C and D (Table 5). Several authors (DeBry & Slade, 1985; Mindell & Sites, 1987; Jansen & Palmer, 1988) have suggested that parallel site gains are much less probable than parallel losses for this kind of data. Trees C and D differ in topology only within *Epilobium*, and of the two, tree D best fits our hypotheses based on geography and morphology. This groups the three morphologically similar species from New Zealand (*Epa-Ebi-Eme*) and places the Himalayan species (*Ero*) with the remaining two species, a position supported by the bootstrap consensus tree (Fig. 2.II). The phylogeny for the other genera in tree D, in which *Circaea*, *Fuchsia*, and *Hauya* are more primitive than *Oenothera* and *Epilobium*, does not contradict evidence from floral and vegetative anatomy and chromosome number and morphology. On the contrary, the position of *Epilobium* as one of the most apomorphic genera is congruent with the specialized chromosome morphology and number (Kurabayashi et al., 1962; Raven, 1976), specialized integument structure (Tobe & Raven, 1985), lobed and commissural stigma (Eyde, 1981), and lack of stipules in *Epilobium*, all characters that have been established as apomorphic in Onagraceae using Myrtales as the outgroup. The bootstrap consensus tree (Fig. 2.II) does not have the same topology as any of the most parsimonious trees, but it is very close to tree D, the only difference being that *Fuchsia* and *Hauya* form a monophyletic group by themselves in the consensus tree.

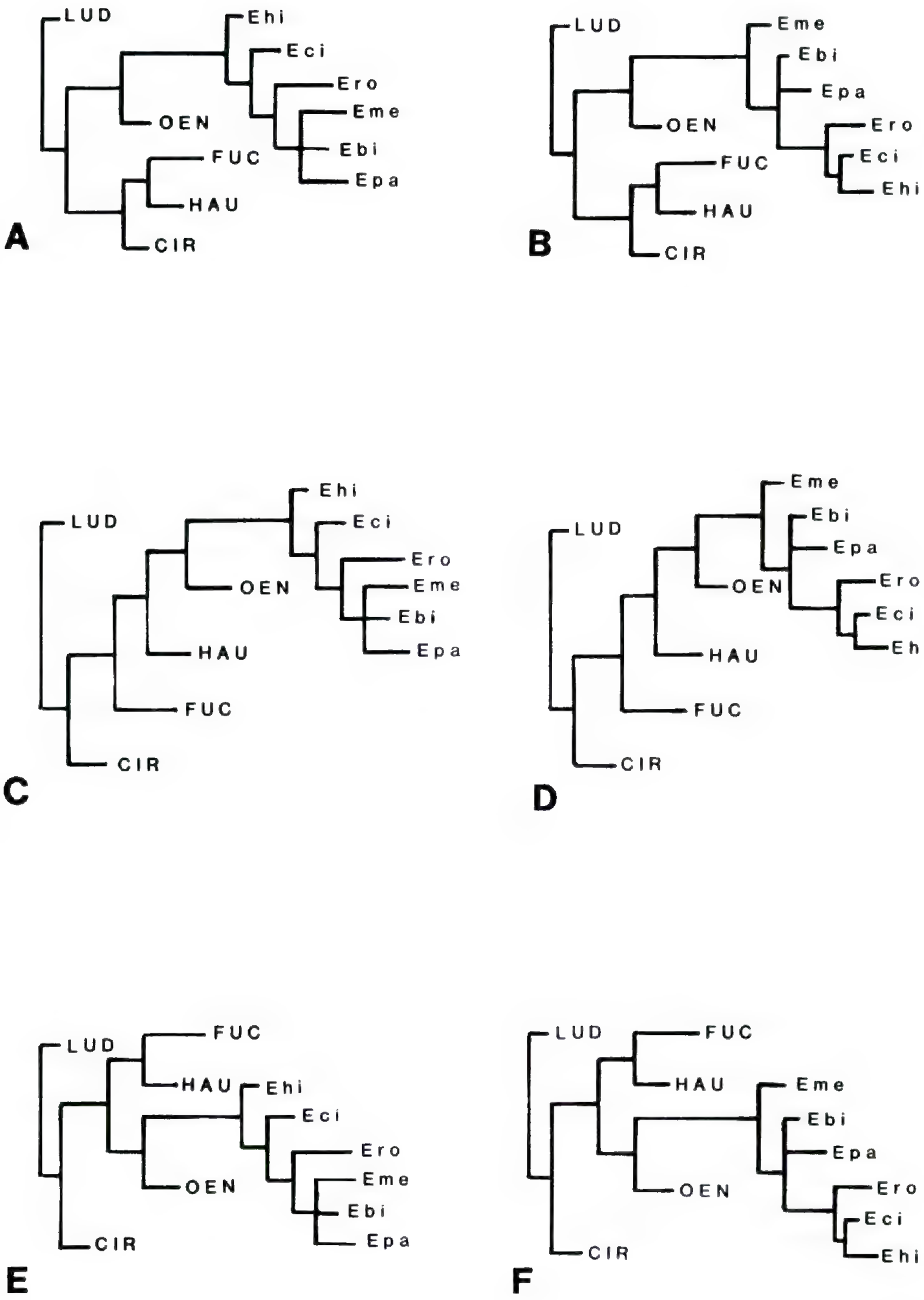

FIGURE 3. Dollo parsimony analysis for 11 species of Onagraceae, using *Ludwigia* as a functional outgroup and based on 65 rDNA restriction site mutations. A–F, six alternative most parsimonious trees; length = 59, consistency index = 0.67.

Morphological data support the position of *Oenothera* as the sister group of *Epilobium* as shown by the Dollo analysis with *Ludwigia* as functional outgroup. In three of the six trees (Fig. 3A, C, E), the phylogeny within *Epilobium* is also supported by morphological data, but the phylogeny in the other three trees (Fig. 3B, D, F) has no such independent support. Morphological data are also less helpful in choosing among the hypotheses for the other genera in the six Dollo trees. Trees C and D have the most conservative phylogeny, with stepwise additions of *Hauya*, *Fuchsia*, and *Circaea* to the monophyletic *Oenothera-Epilobium* group. Trees E and F differ in making *Fuchsia* and *Hauya* a monophyletic group, leaving *Circaea* as sister group to the rest of the taxa. Tree A, in which the monophyletic group (*CIR*(*HAU-FUC*)) forms a sister branch to *OEN-EPI*, and which includes the favored phylogeny in *Epilobium*, is nearly coincident with the bootstrap consensus tree (Fig. 4),

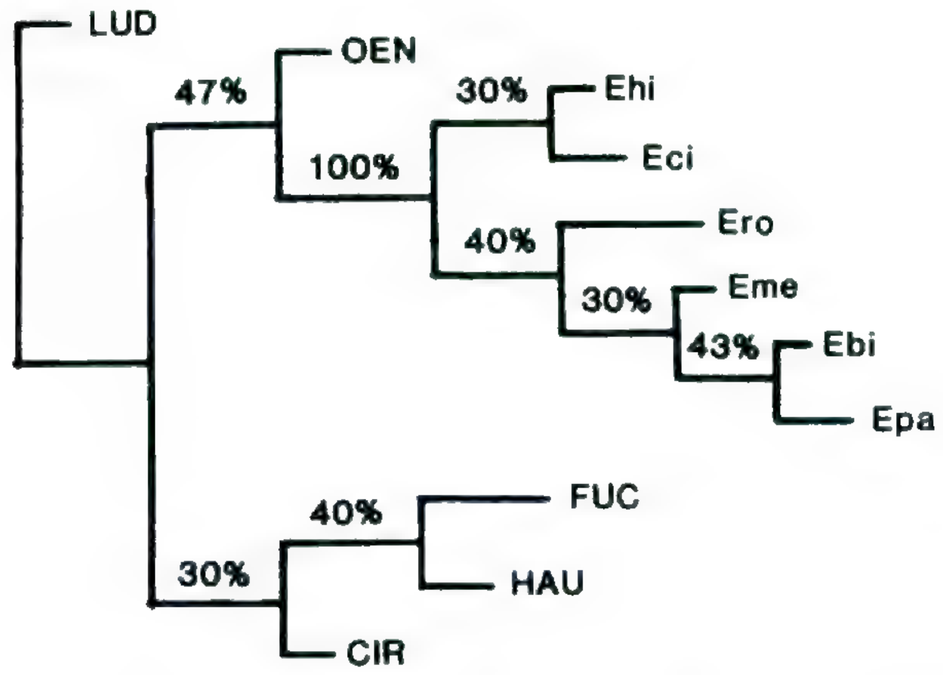

FIGURE 4. Dollo parsimony analysis for 11 species of Onagraceae using *Ludwigia* as functional outgroup. Majority-rule consensus tree constructed from 100 bootstrap samples. Percentages are as in Figure 2.

differing only in that *Eci-Ehi* form a monophyletic group in the consensus tree. Several authors, as noted above, argue that Dollo parsimony is a more consistent and efficient estimator of phylogenetic relationships for restriction site data because parallel site losses are much more probable than parallel site gains. Based on these considerations, we prefer tree A of the Dollo analysis as the most likely geneological hypothesis for the taxa we have included. Figure 6 shows this hypothesis, with the characters superimposed on the tree; there are no parallel gains or loss-gains.

Wagner analysis can generate a tree of the same topology that is only 2 steps longer than the most parsimonious ones, but there are at least 300 trees of equal or shorter length.

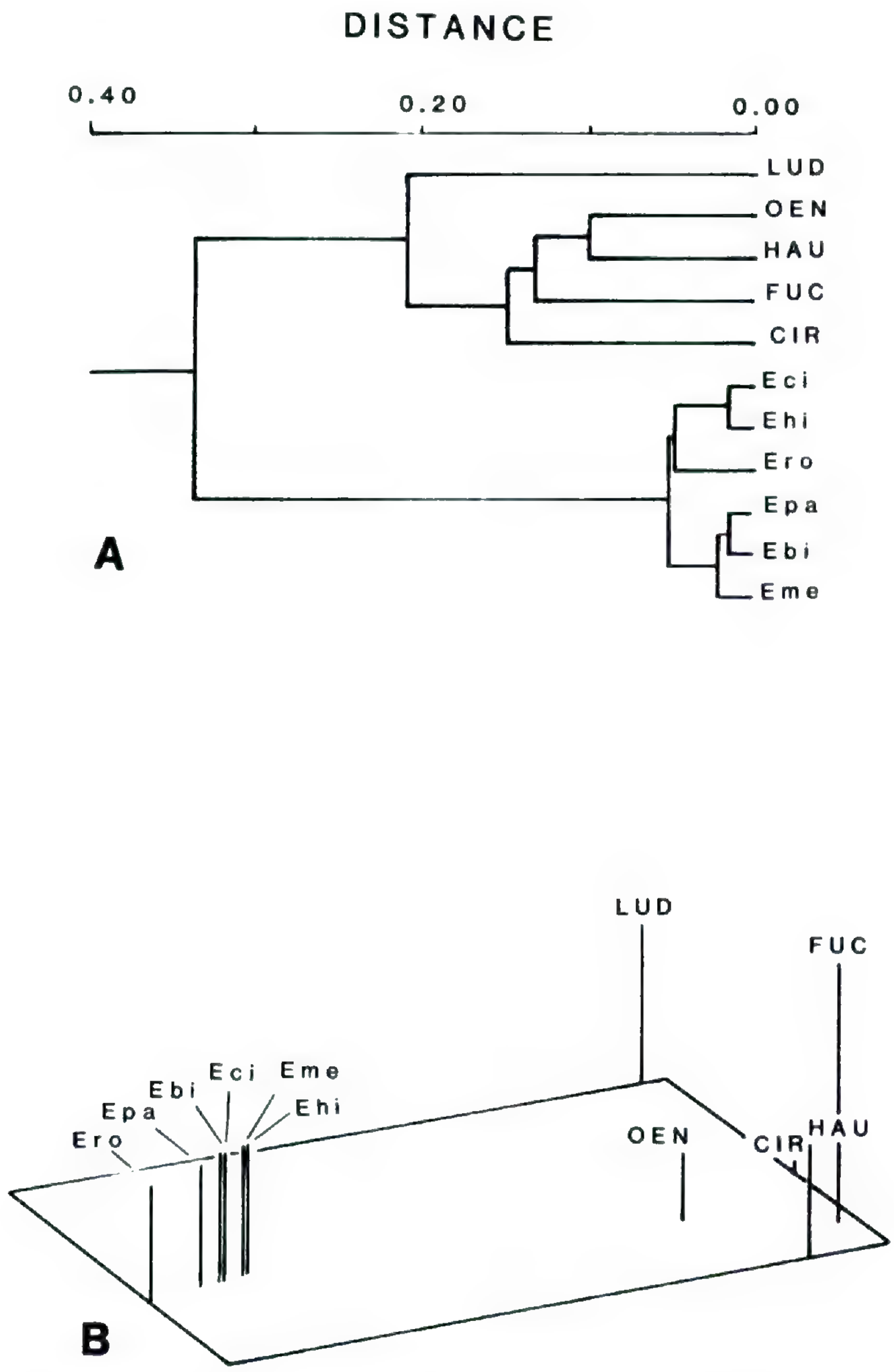

FIGURE 5. Phenetic analysis of 11 species of Onagraceae based on 65 rDNA restriction site mutations.—A. Phenogram of 11 OTUs resulting from UPGMA cluster analysis of the OTU × OTU Manhattan distance matrix. —B. Principal coordinate analysis. Perspective three-dimensional projection of the OTUs on the axes representing the first three factors. The percentages of variation explained by each of the three factors are: I = 83.71%; II = 10.04%; and III = 4.39%. The total variation explained by the model is 98.14%.

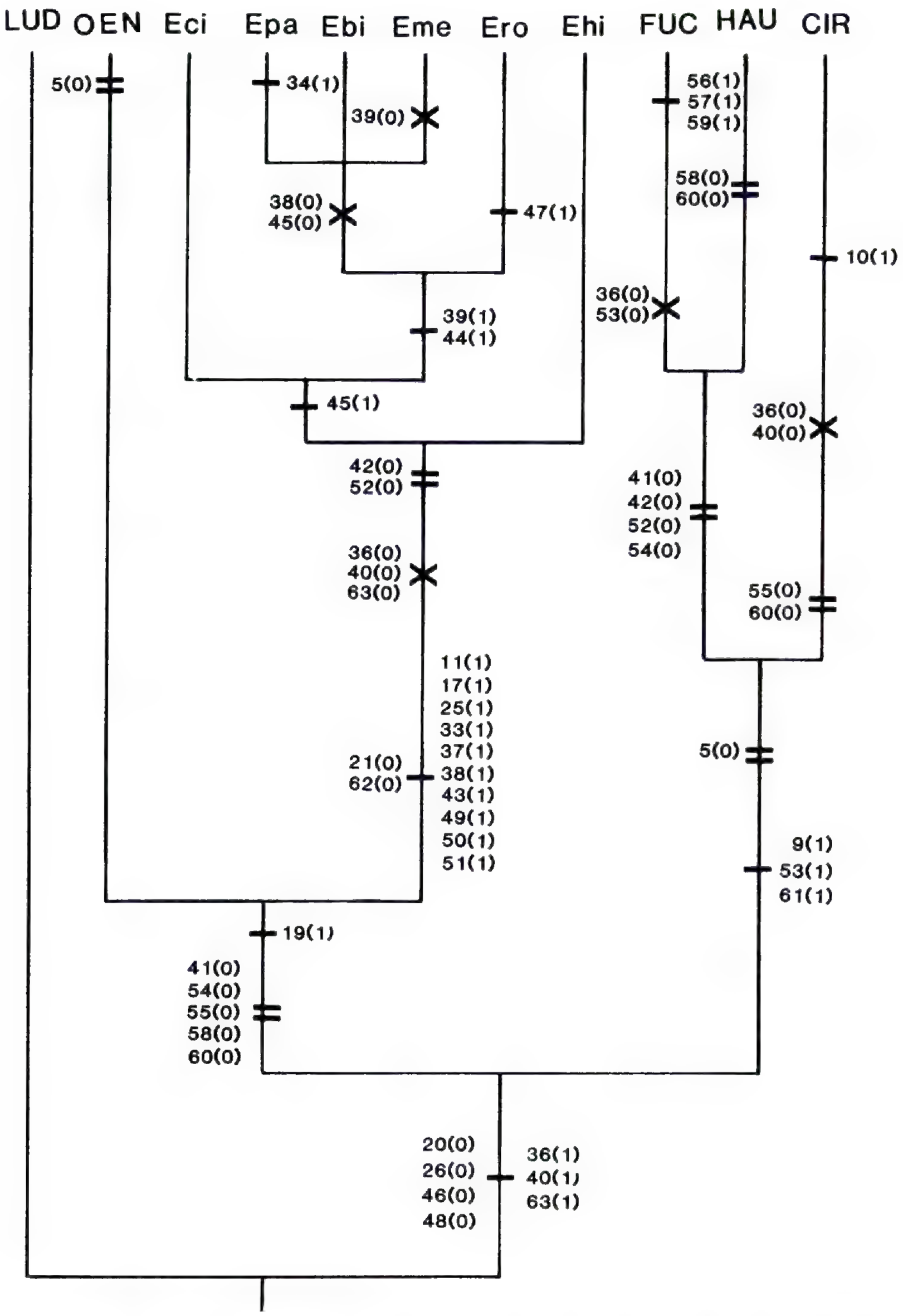

FIGURE 6. Phylogenetic hypothesis (one of six most parsimonious trees) from Dollo parsimony analysis using *Ludwigia* as functional outgroup and based on variation in rDNA restriction sites. Restriction site gains (1) and losses (0) are superimposed onto the tree; single line = synapomorphies; double line = parallel or convergent evolution, X = reversals. Note that all homoplasious changes are parallel losses or gains/losses. Constant characters have been excluded from illustration.

PHENETIC ANALYSIS

The results of phenetic analysis using either cluster analysis or principal coordinate analysis (Fig. 5) demonstrate: (1) the extreme distinctness of *Epilobium*; (2) a fairly great distinctness of *Ludwigia*; and (3) strong clustering of *Epilobium* species. We can attribute the extreme distinctness of *Epilobium* within the family in the phenetic analyses to the possibility of different evolutionary rates in Onagraceae. Since the algorithms for phenetic techniques are usually rate-dependent (Hillis, 1987; Ruvolo, 1987), they are more likely to produce spurious results than are rate-independent methods such as Wagner or Dollo analysis.

The groupings of *Epilobium* species (e.g., close clustering of *Eme-Ehi* and *Eci-Ebi*) by principal coordinate analysis are contrary to relationships suggested by both morphological and cytological data (Raven & Raven, 1976). Rohlf (1968) has noted that distances between close neighbors are not well represented by ordination techniques.

Conclusions

One limitation of this study is related to the use of restriction maps rather than nucleotide sequence data. The restriction sites analyzed involve only about 5% of the total base pairs (ca. 390/8000+ bp) in the rDNA repeat unit of Onagraceae, and the only changes that can be detected involve gain or loss of a recognition sequence at a site and major changes in repeat length. Loss of restriction sites can be accomplished by changes at any of the six nucleotides in the recognition sequences, so the acquisition of parallel, nonhomologous losses is relatively likely. However, the relative likelihood of various convergent events is fairly well understood (Hillis & Davis, 1986; Templeton, 1983a, b), so certain tree-construction algorithms (e.g., Dollo parsimony) can correct for inherent biases in the data set. Furthermore, the extent of homoplasy within rDNA analysis is limited by the conservative nature of rDNA. Therefore, despite the small sample size of actual base pairs examined, restriction-site mapping provides valuable data for phylogenetic reconstruction.

The lack of restriction site variation among samples of three populations of *Epilobium melanocaulon* suggests that the consistency of the restriction site data is high. The six species of *Epilobium* always cluster together, regardless of the algorithm applied to the data, and when bootstrap methods are applied, the monophyletic *Epilobium* group appears 100% of the time. This gives us confidence in the robustness of restriction site data as taxonomic characters.

It is also possible to evaluate the relative performance of the different algorithms in analyzing our data set. As expected for restriction site data, Dollo parsimony gives better results than Wagner parsimony, when compared with the previous knowledge of Onagraceae. As noted by Jansen & Palmer (1988), however, Dollo parsimony is too rigid because it completely prohibits parallel gains, and although convergent gains have a very low probability, they can occur occasionally. A parsimony algorithm that gives differential weights to homoplasious gains versus losses would be preferable.

The main difference between the phylogenetic analyses and the phenetic analyses rests on the extreme distinctness of *Epilobium* in the latter. Independent data from morphology, anatomy, and protein sequence analysis strongly support the results of phylogenetic analyses. Therefore, the anomalous results of the phenetic analyses seem to reflect a different evolutionary rate in *Epilobium* compared with the other genera and the greater sensitivity of phenetic analyses to this phenomenon.

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NEW CONSIDERATIONS REGARDING THE CORONA IN THE VELLOZIACEAE[1]

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and João Semir[3]

Abstract

Subfamily Barbacenioideae of the Velloziaceae is characterized by sessile anthers that are connected to a corona (or to the upper part of the hypanthium). *Barbacenia spiralis* L. B. Smith & Ayensu, however, displays a characteristic that distinguishes it clearly from the rest of the Barbacenioideae. It has stamens in which the filaments and anthers are totally independent of the corona lobes. This feature is considered important enough to justify the recognition of a new genus, based on this species.

Menezes (1970, 1973) concluded that the petaloid appendices found in the genus *Barbacenia* (Vandelli, 1788) and described as "flattened filaments" by the latter author and all later specialists of the family Velloziaceae, including Smith (1962), should in fact be regarded as lobes of a corona, as in *Narcissus* (Amaryllidaceae).

Studies of the floral vascular tube of many species belonging until then to *Barbacenia* showed the vascular bundles of the petaloid appendices to diverge from petal and sepal traces in the upper part of the hypanthium and to display an inversion (Menezes, 1970, 1973). A similar inversion of tissues was observed by Arber (1937) in the corona of the Amaryllidaceae, where the xylem of the corona bundles is turned toward the xylem of the petal (or sepal) bundles, and the phloem is internal to the xylem.

According to the available evidence, if the petaloid appendices were "flattened filaments," then their vasculature should consist of bundles originating from the staminal trace. But this is not the case: not only do the bundles of the corona originate in the perianth, but the staminal trace itself passes through the inside of the corona without any alteration in its concentric structure before penetrating the anther (Menezes, 1970, 1973, 1984).

Other authors have attempted to explain the nature of these petaloid appendices. On the basis of external morphology, Noher de Halac & Cocucci (1971) interpreted them as staminodes. Smith & Ayensu (1976), while admitting that either the staminode concept of Noher de Halac & Cocucci or the corona concept of Menezes might be correct, adopted the term "coronoid appendices" (Smith & Ayensu, 1976, 1980) in partial support of Menezes's hypothesis.

The present work considers the consequences on generic delimitation within subfamily Barbacenioideae Menezes of our new observations on *Barbacenia spiralis* Smith & Ayensu.

Materials and Methods

The following plant material was collected for analysis: *Barbacenia spiralis* L. B. Smith & Ayensu, Brazil. Mato Grosso: Muncipio de Diamantina, Curralinho, 13 Nov. 1980, *Menezes 1043* (SPF). *Pleurostima plantaginea* (L. B. Smith) Menezes, Brazil. Mato Grosso: Serra do Cipó at km 128, 14 July 1971, *Menezes 129* (SPF).

Anatomical studies were based on serial sections of material fixed in FAA 50 (Johansen, 1940) and embedded in paraffin. Sections were stained with safranin and fast green (Sass, 1951).

Results

As the basic pattern of vascularization in the Velloziaceae has previously been described in other species by Menezes (1973), only aspects relevant to *Barbacenia spiralis* are described here.

Figure 1 shows a flower of *Barbacenia spiralis*,

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which is sectioned in Figure 2. The filament (Fl) is completely free from the corona (Co) lobe, and a descending basal region (Dbr) of the filament can be seen; the anther (An) is basifixed. The auriculate and sessile anther (An) is attached to the corona lobe in *Pleurostima plantaginea* (Fig. 3). The anther is easily detached (Fig. 4) and is accompanied by the filament tissues (Af), which are superficially adnate to the corona.

In *Barbacenia spiralis* (Figs. 5–16) the petal staminal traces (Ps) are situated opposite the petal–corona complex (Cpc), which divides into a branch that enters the petal (P) and to one that runs into the corona (Co). The ventral bundle of the carpel (V) and the stamen–carpel complex (Sc) originate from the same basic bundle, situated at the base of the ovary. The stamen–carpel complex also gives rise to the dorsal bundle of the carpel (D) and the stamen trace opposite the sepal (Ss).

In the peduncular region of the flower (Fig. 6) there are 12 fundamental bundles (Fb). Further up (Fig. 7), the locules still have no ovules, but septal nectaries (Sn) appear. At the level of Figure 8 the placentas bear ovules, and nectariferous sacs (Ns) can be observed. The ventral bundles of the carpel (V), the dorsal bundles (D), the traces of the sepalar (Ss) and petalar (Ps) stamens, and of the petal–corona (Cpc) and sepal–corona (Csc) complexes are now distinct. The septal nectaries follow the locules right from the base (Fig. 7), and even when the locules (Lo) close (Fig. 11), the nectariferous sacs remain wide open (Ns; Figs. 10, 11). In Figure 12 a descending basal region (Dbr) of the filament (less prominent than in Figs. 2 and 5) is seen. This brings the filament (Fl; Figs. 13, 14) close to the style (St). Figure 12 also shows the individualization of two corona lobes (Co). At the level of Figures 14 and 15, the petals, sepals, petalar and sepalar lobes of the corona, and the filaments of petalar and sepalar stamens are all clearly distinct. At a higher plane (Fig. 16) the corona lobes are no longer visible. The anthers are introrsely dehiscent, although three anthers appear to be extrorsely dehiscent due to twisting of the filaments.

Figures 17–20 show details of the vascularization displayed in Figures 5–16. In Figure 17 divergences (Dv) of the sepalar traces to form the corona traces (Ct) may be seen. Figures 18–20 show a single plane at different scales. The region indicated by two dotted lines in Figure 18 is shown in greater detail in Figure 19; Figure 20 shows a magnified portion of Figure 19. In Figure 20 the corona bundle (Cb) shows inversion of the vascular tissues: the xylem (X) is turned outward to face the xylem of the petal (P), while the phloem (Ph) is internal to the xylem.

Discussion

Barbacenia spiralis was first described based on a specimen with only a flower bud. For this study, the species was collected in full flower. If there were any remaining doubts as to the true nature of the petaloid appendices in subfamily Barbacenioideae, they can now be put to rest, since in this species, the filaments and corona lobes are completely separate. The origin and inversion of the bundles indicate that the corona is an appendage of the perianth; there is, furthermore, a complete independence of stamen and corona. This feature is unique to Barbacenioideae, which contain some 106 species in three genera. All except *B. spiralis* have sessile anthers (basifixed-auriculate or dorsifixed) adnate to the corona in *Barbacenia*, *Aylthonia*, and *Pleurostima* sect. *Graziela*, or to the hypanthium in sect. *Pleurostima* (Menezes, 1980b).

According to the circumscription of Barbacenioideae proposed by Menezes (1970, 1971), the sessile anther connected to the corona lobe is a fundamental character. Studies of leaf anatomy (Menezes, 1970, 1975) permitted the addition of a further fundamental character for Barbacenioideae: the presence of a double sheath in the vascular bundles of the leaf (Menezes, 1980a, b, 1984). In subfamily Vellozioideae, the bundle sheath is simple and each anther is connected to a filament, although this filament may at times be inconspicuous (Menezes, 1980a, b).

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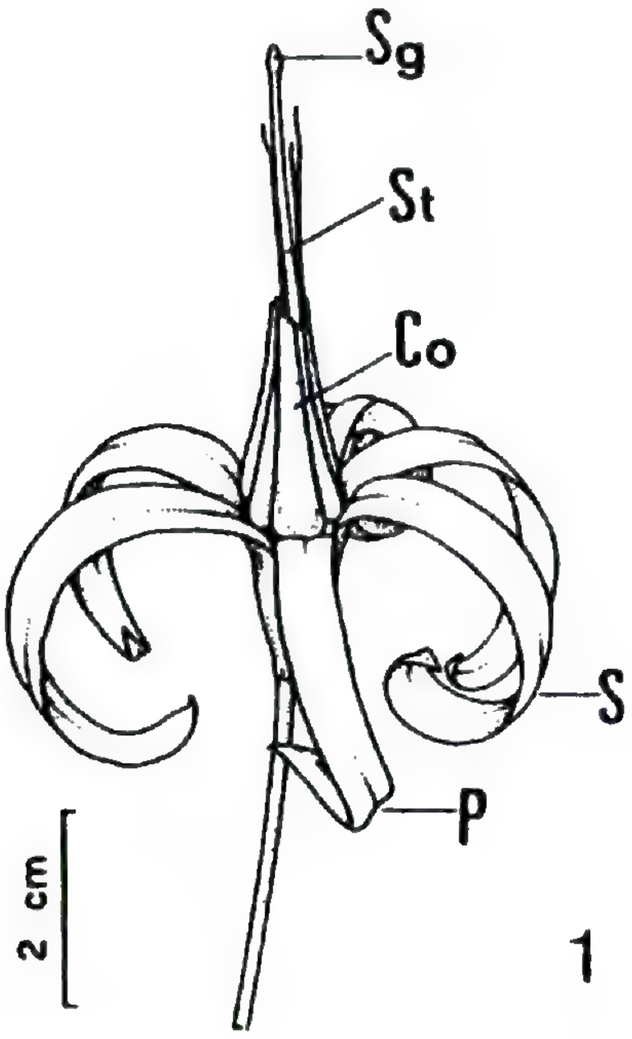
Figures 1–4. Flowers of *Barbacenia spiralis* and *Pleurostima plantaginea*. 1, 2. *B. spiralis*.—1. Flower with flexed petals (P) and sepals (S), and corona lobes simulating a tube.—2. Longitudinal section through flower revealing stamen with basifixed anther on a cylindric filament (Fl) that is independent of the corona and has a descending basal region (Dbr) below the terete portion. 3, 4. *Pleurostima plantaginea*.—3. Petal and corona lobe with the basifixed-auriculate and sessile anther (An).—4. Anther separated from the corona, showing the previously adnate filament (Af) free from the corona lobe. Au—auricle; Hy—hypanthium; Sg—stigma; St—style.



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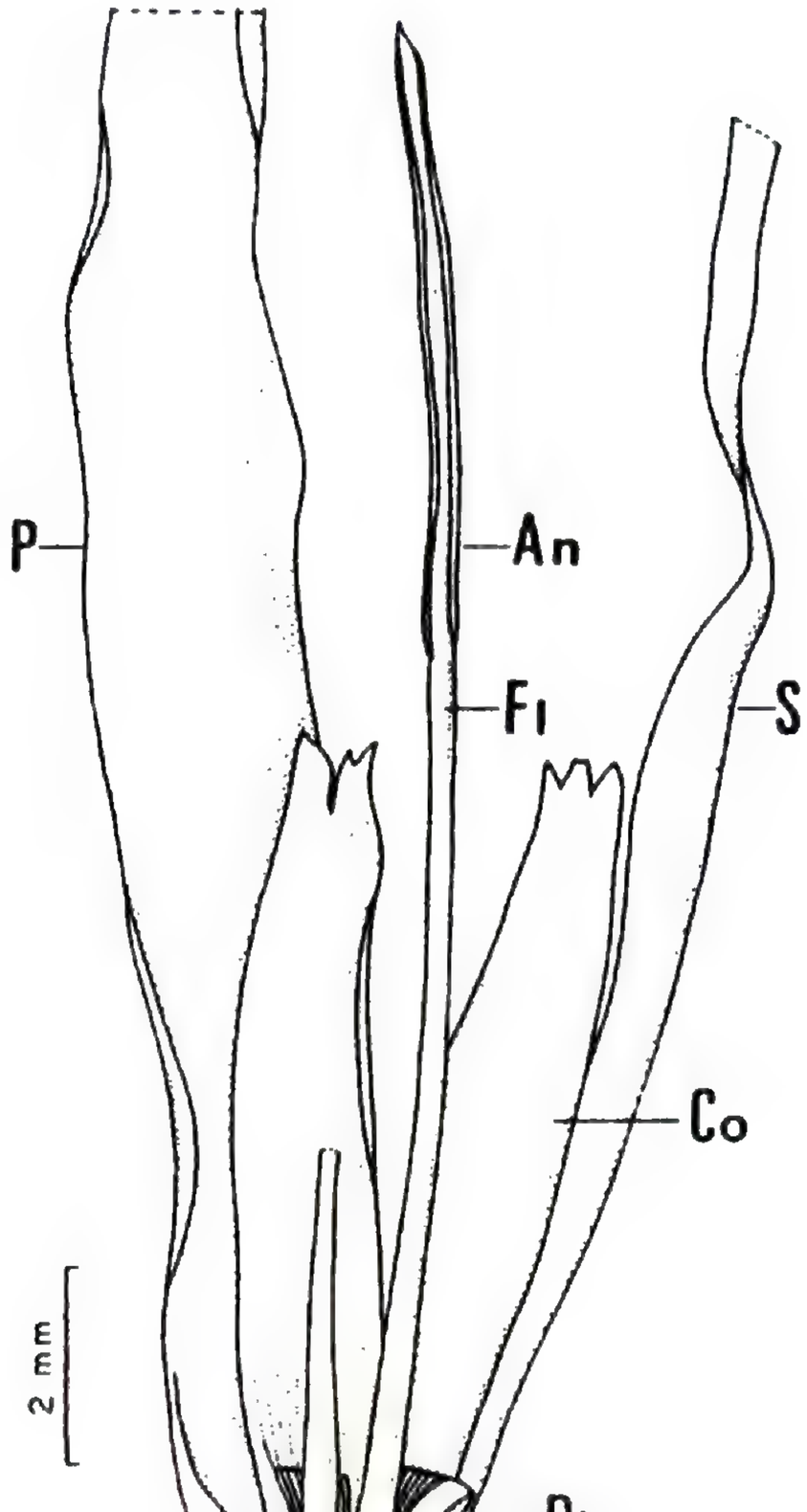

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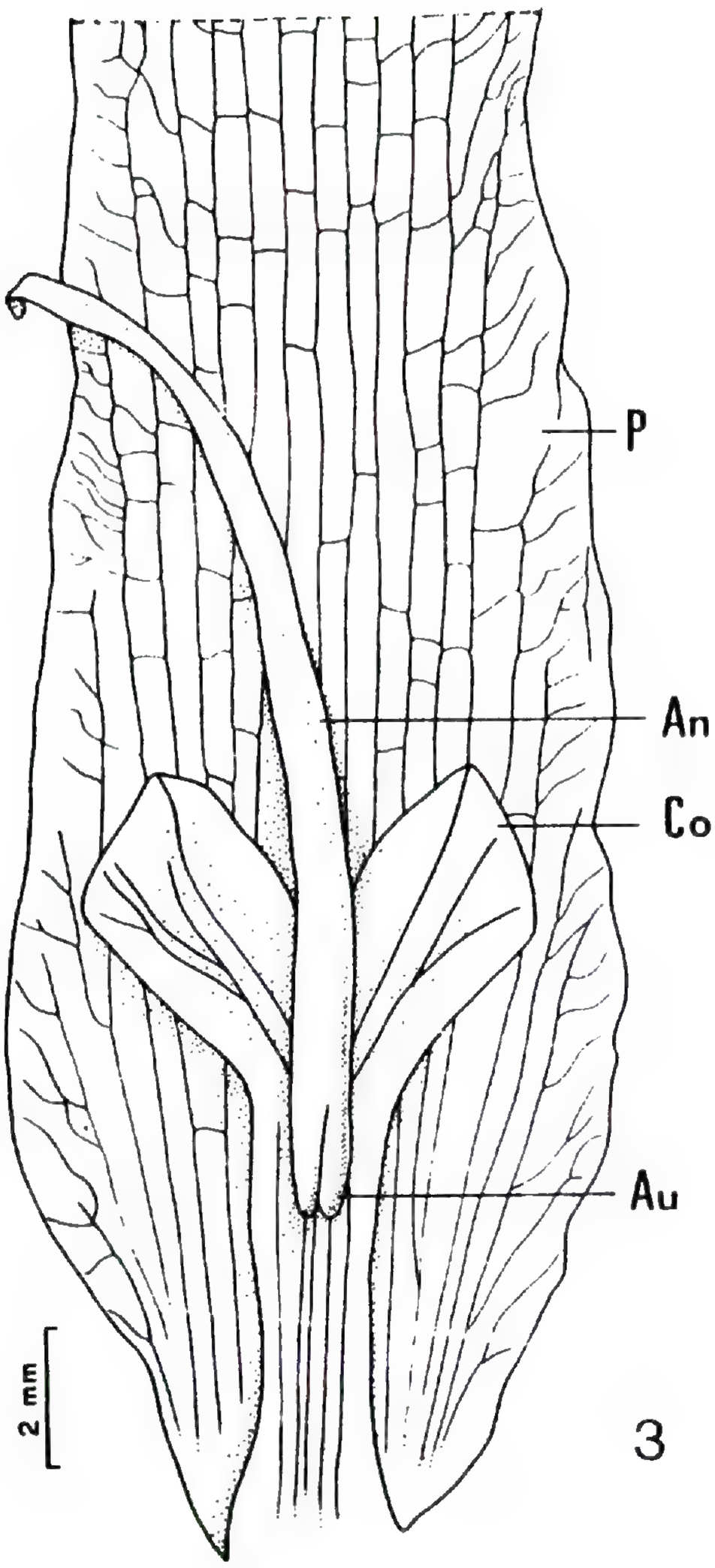

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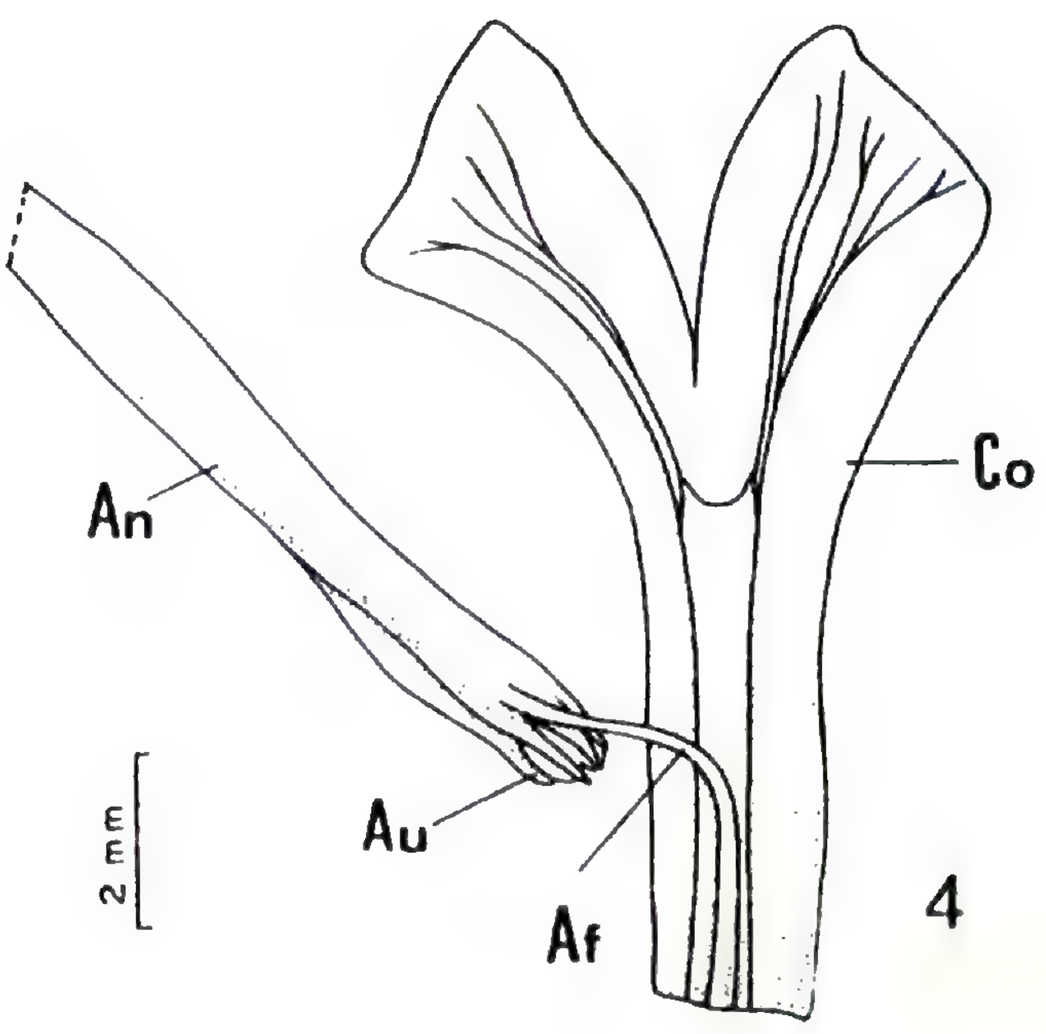

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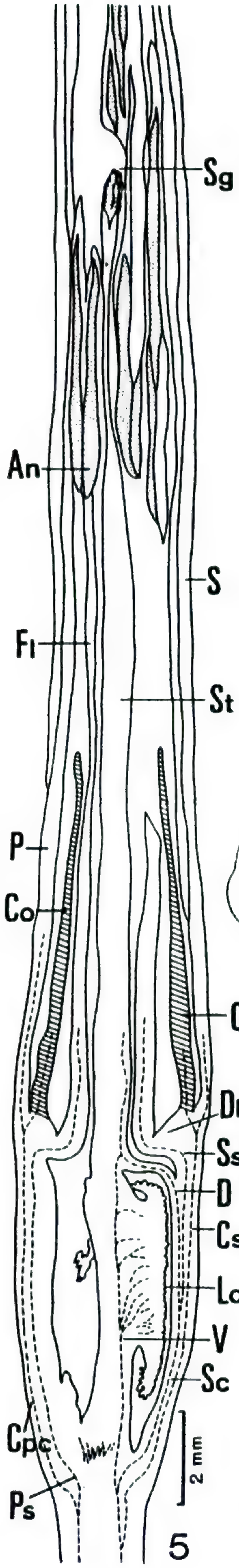
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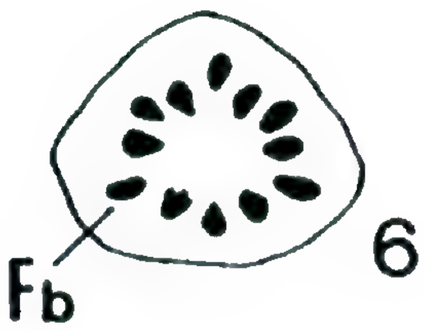
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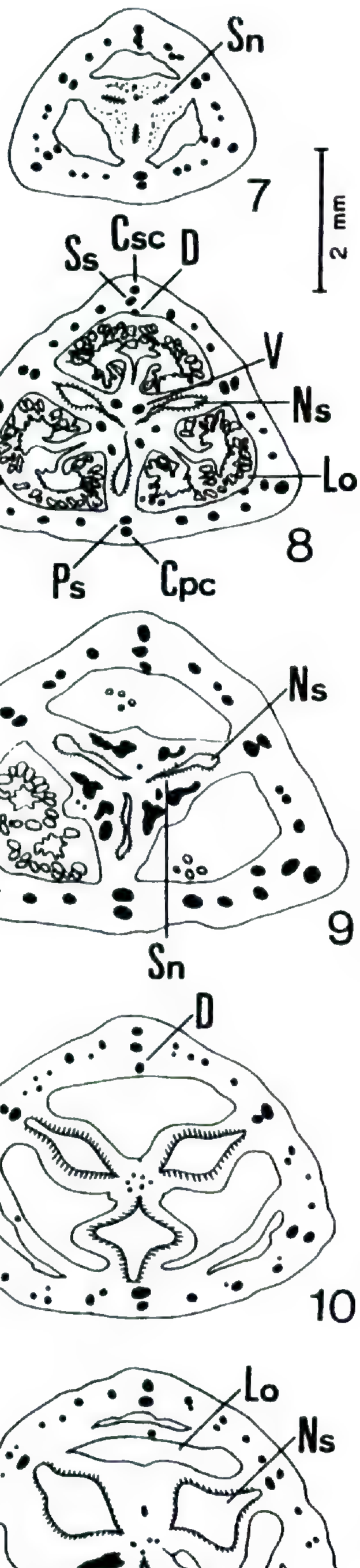
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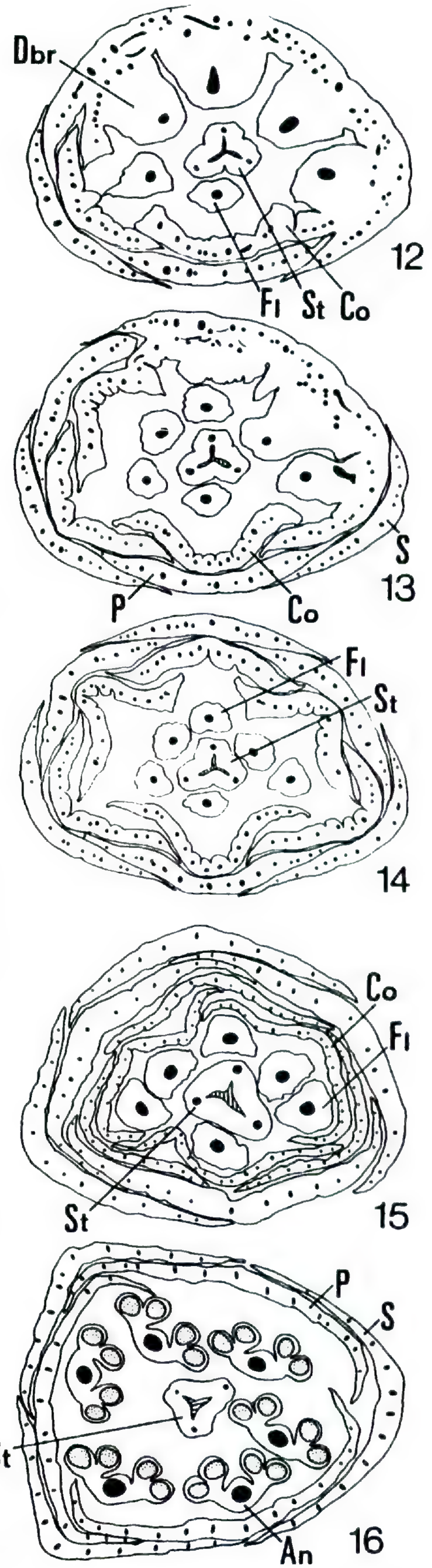
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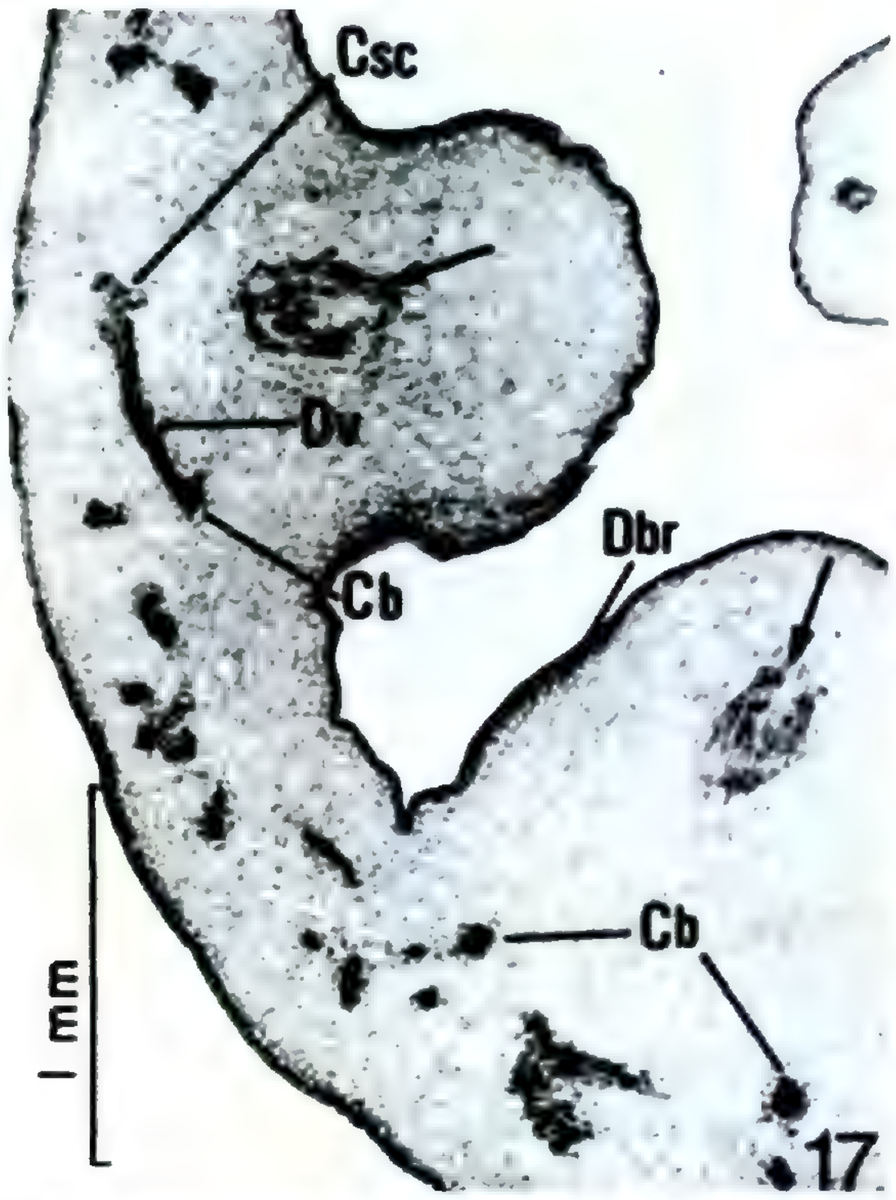

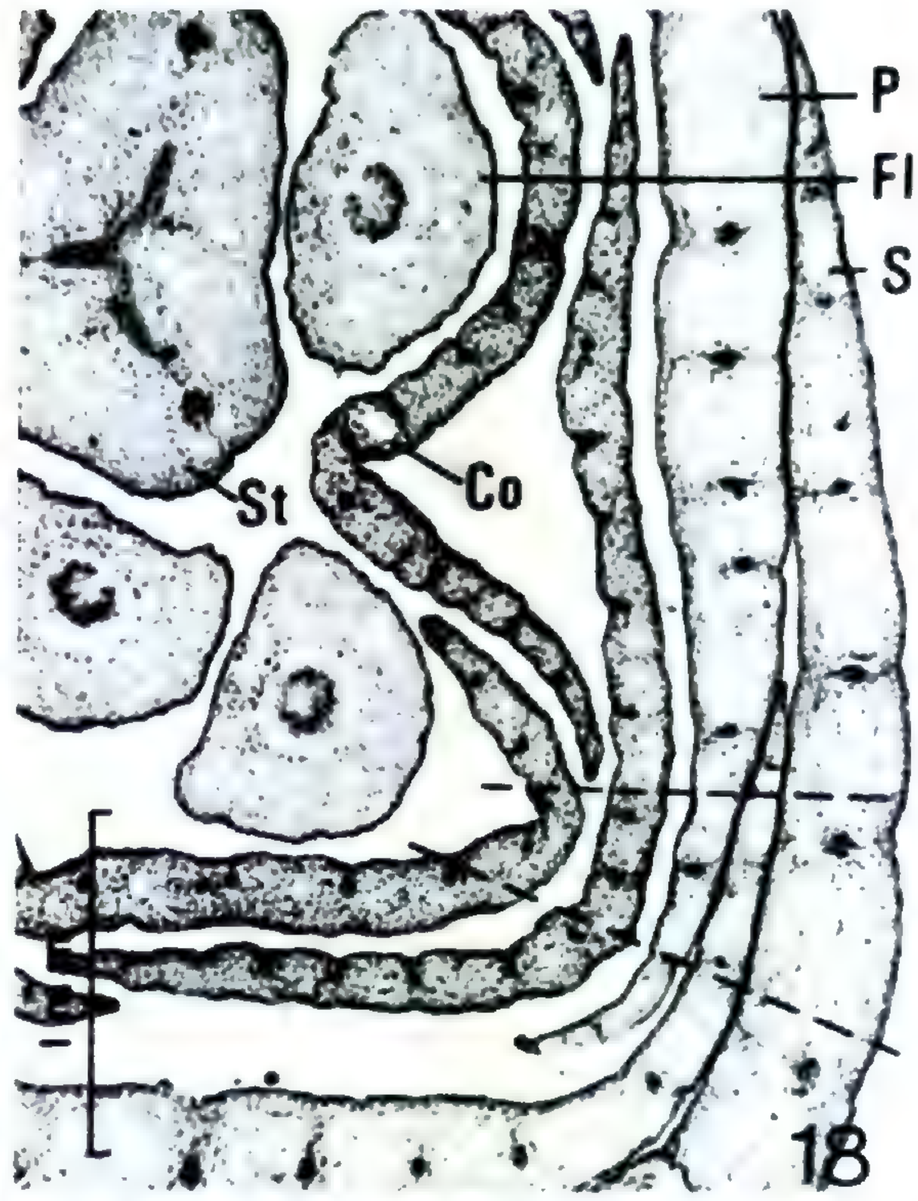

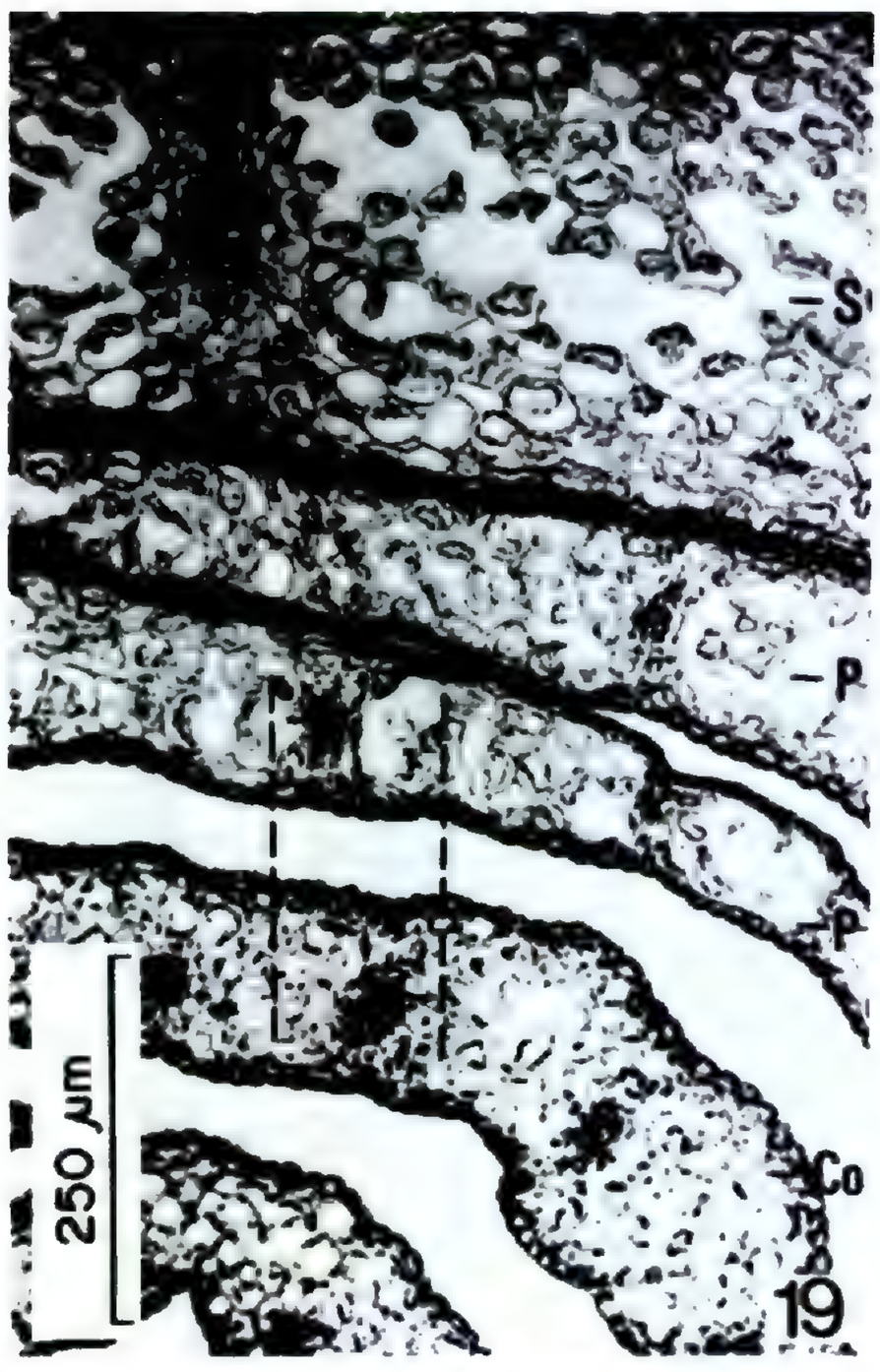

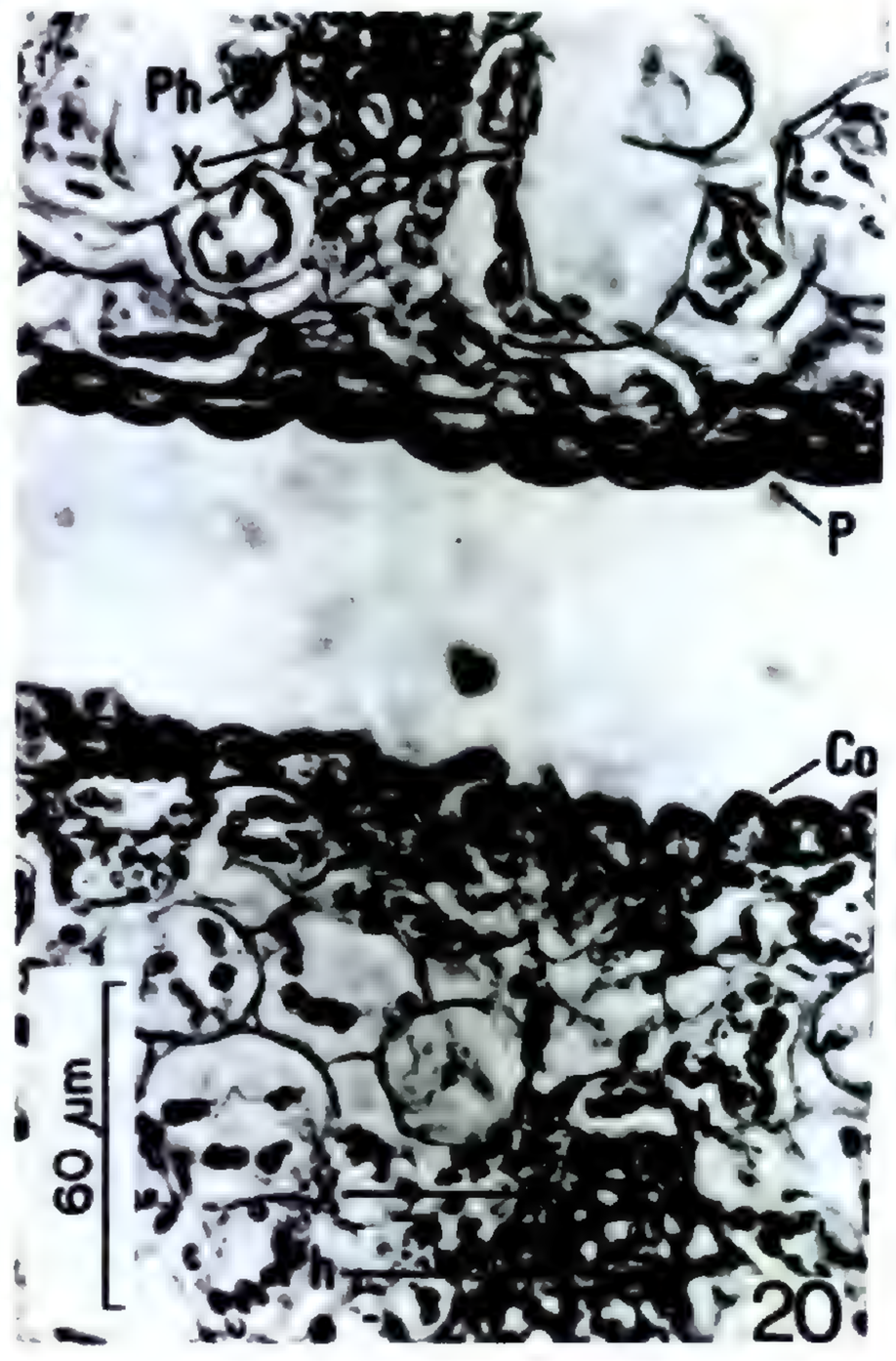

FIGURES 17–20. Details of the vascularization of *Barbacenia spiralis* flower bud.—17. Divergence of the corona trace (Dv) from the sepal–corona complex (Csc). The corona bundles (Cb) are not attached to the stamen bundles (arrows).—18. Cross section of flower bud with corona lobes (Co) independent of filaments (Fl).—19. Enlargement of the portion of Figure 18 between the dashed lines.—20. Enlargement of portion of Figure 19 between dashed lines; the xylem (X) is turned outward and the phloem (Ph) is internal to the xylem. Hy—hypanthium; P—petal; S—sepal; St—style.

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FIGURES 5–16. Floral vascularization of *Barbacenia spiralis*. See text for explanation of figures. An—anther; Co—corona; Cpc—petal–corona complex; Csc—sepal–corona complex; D—carpel dorsal bundle; Dbr—descending basal region; Fb—fundamental bundle; Fl—filament; Lo—locule; Ns—nectariferous sacs; P—petal; Ps—petalar stamen trace; S—sepal; Sc—stamen–carpel complex; Sg—stigma; Sn—septal nectary; Ss—sepalar stamen trace; St—style; V—carpel ventral bundle.

Barbacenia spiralis has a well developed filament and a basifixed anther (without auricle), as in *Vellozia* (Vellozioideae); the flower, however, has a corona, and the leaf bundle sheath is double (endodermic internally, and externally a sheath derived from a mesophyll) as in the Barbacenioideae.

Thus *B. spiralis*, although belonging to Barbacenioideae, shows some intermediacy. Probably, free filaments should be considered ancestral to adnation of the filament to the corona seen in all other species of Barbacenioideae.

Other intermediate conditions are known: in *Pleurostima plantaginea* the filament is not deeply fused to the corona lobe, which thus shows a similar but presumably independently derived condition.

The filament independent of the corona lobe and auricle-free basifixed anther with distinct dehiscence (Menezes, 1988) by themselves justify the description of a new genus based on this species, which will be the subject of a forthcoming paper (Menezes & Semir, in prep.).

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ADDITIONAL TRANSFERS OF ASIATIC *MACHILUS* SENSU NEES, NON DESROUSSEAUX, TO *PERSEA* MILLER (LAURACEAE)

A. J. G. H. Kostermans[1]

In 1962 I reviewed the genus *Machilus* sensu Nees in Asia, relegating the species known at that time to *Persea* because there is not the slightest difference between *Machilus* Nees and *Persea* Miller. This can be easily demonstrated by comparing the drawings of the American *Persea* (Kopp, 1966) and those of Chinese *Machilus* (Lee, 1979).

The name *Machilus* goes back to the pre-Linnean Rumphius, *Herbarium Amboinense 3* (1743), a latinization of the vernacular name makilan (which is perhaps the general name for lauraceous trees, like medang in the greater part of Indonesia).

Rumphius described initially two species of *Machilus*, which he called the male and the female. The "male" is depicted on plate 40 and represents *Litsea glutinosa* (Lour.) C. B. Robinson.

Of the "female" a leaf is shown on the same plate 40; it is certainly not the "male." It might not belong to Lauraceae.

Rumphius added two more species on page 70, of which the third one, depicted on plate 41, represents *Dehaasia media* Bl. The fourth one, called the smallest by Rumphius, which I formerly thought to be a real *Machilus*, is not lauraceous, as is evident from the presence of five perianth lobes and the shape of the fruit; it might be *Ilex*. Merrill's (1917) suspicion that this should be a species of *Phoebe* is not accurate.

Thus Rumphius's *Machilus* is a mixture of a *Litsea*, a *Dehaasia*, and two non-Lauraceae. The Rumphian species were validated under the name of *Machilus* by Desrousseaux (1791) in Lamarck's Encyclopédie (3: 668). No type species was indicated.

As the "male" (*Litsea glutinosa*) is the most elaborately described, we accept it as the lectotype.

Litsea Lamarck was published a few pages earlier (p. 574) and hence takes priority. If this is not acceptable, *Litsea* Lamk. should be conserved against *Machilus* Desrousseaux.

Machilus turned up again as a generic name in 1831 as adapted by Nees. Nees's species were based on herbarium material of plants from India, Sumatra, and the Malay Peninsula. He incorrectly added Rumphian names in synonymy; they do not invalidate Nees's names.

Hence, as I have pointed out (1962), Nees's *Machilus* is a later homonym of that of Desrousseaux. Whether Nees was unacquainted with Desrousseaux's publication is unknown.

Machilus sensu Nees was described with four species (no type indicated). The first, *Machilus odoratissimus* Nees, based on an Indian specimen, should be accepted as the type species of Nees's genus. Nees's addition of the synonym *Machilus quarta* Rumphius is a mistake. The second species, *M. macranthus*, likewise belongs to *Machilus* sensu Nees. The third one, with the Rumphian synonym *M.* "*tertia media*," is *Dehaasia media* Bl. The fourth species, *M. incrassatus* Nees, was based on *Laurus incrassatus* Jack and was relegated by Nees first to *Persea* and later moved to *Haasia*. Its correct name is *Dehaasia incrassata* (Jack) Kosterm.

Machilus sensu Nees was accepted by Meissner (1864), but wrongly ascribed to Rumphius, whereas Desrousseaux is not mentioned. Baillon (1872), Bentham & Hooker (1880), Pax (1889), Allen (1936), and Chinese students of Lauraceae (Lee, 1979) likewise accepted *Machilus* sensu Nees, unaware of the existence of *Machilus* Desrousseaux. I suggested in 1962 that *Machilus* sensu Nees was congeneric with *Persea* Mill.

All Asiatic species belong to sect. *Machilus* Kopp. *Persea* is very similar to *Phoebe* Nees, non Mez, but the latter in the fruiting stage has enlarged, thickened, yellowish, erect perianth lobes, clasping tightly the black, ovoid, gradually pointed fruit. In *Persea* the lobes are not enlarged, not thickened and reflexed or completely deciduous in sect. *Machilus*; other American species have persistent, indurate not or little enlarged nonerect perianth lobes in the fruiting stage and might be referred to a different genus.

[1] Herbarium Bogoriense, Jalan Juanda 22, Bogor, Indonesia.

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NEW OR NOTEWORTHY ORCHIDS FOR THE VENEZUELAN FLORA. VIII. NEW SPECIES AND COMBINATIONS FROM THE VENEZUELAN GUAYANA[1]

Germán Carnevali[2,3] *and*
Ivón Ramírez[2,3]

ABSTRACT

In preparing the treatment of the Orchidaceae for the *Flora of the Venezuelan Guayana*, several new taxa have been detected. These include specimens from recently completed expeditions and earlier herbarium material. Reconsideration of generic boundaries within several subtribes has made necessary various nomenclatural changes. The following new taxa and combinations are proposed: *Cleistes huberi*, sp. nov.; *C. rosea* f. *pallida*, f. nov.; *C. unifoliata*, comb. nov.; *Octomeria romerorum*, sp. nov.; *Pleurothallis deborana*, sp. nov.; *P. pemonum*, sp. nov.; *Stelis garayi*, comb. nov.; *Sobralia oliva-estevae*, sp. nov. In addition, comments are supplied, where pertinent, on the affinities of the various taxa proposed.

The Orchidaceae are the largest of all flowering plant families, with probably more than 25,000 species. Its range is worldwide, but it is especially diverse in the tropics of both hemispheres (Dressler, 1981). It is also the largest family of plants in the Venezuelan Guayana, accounting for about 750 species now recognized; new taxa are constantly being added as new explorations are carried out. Our estimates suggest that this figure will eventually rise up to 800 or more once the whole area is well botanized. In this article six new taxa are described as the result of recently completed field trips or the study of earlier herbarium material. Furthermore, reconsideration of generic boundaries within several subtribes have made various nomenclatural changes necessary.

CLEISTES

The genus *Cleistes* L. C. Rich. consists of about 30 species (Dressler, 1981), widely ranging through the American tropics and subtropics, with a concentration of taxa in southern Brazil. This genus is closely related to *Pogonia* Juss., from which it differs by having pollen grains coherent in tetrads. Some authors do not recognize both genera as distinct (Foldats, 1969), but most recent authors have preferred to retain the neotropical group *Cleistes* as a distinct entity. Nine species of *Cleistes* are known from Venezuela, eight of them occurring in the Venezuelan Guayana; one of these is newly described.

Cleistes huberi Carnevali & I. Ramírez, sp. nov.

TYPE: Venezuela. Bolívar: Aparamán-tepui, westernmost of four tepuis in the Aparamán Range, 2,150 m, 5°54′N, 62°07′W, summit of highly eroded sandstone mesa, 22 Mar. 1987, *B. Holst 3480* (holotype, VEN; isotype, MO). Figure 1.

Species haec *Cleistes strictae* C. Schweinf. proxima sed statura vegetativa et florali minore, labello trilobato recedit.

Small, erect, heliophilous, terrestrial or subterrestrial herbs, 4–15 cm high, solitary or growing in small, loose colonies. Tubers ellipsoid, 1–1.5 cm long and wide. Stems subterete, erect, straight

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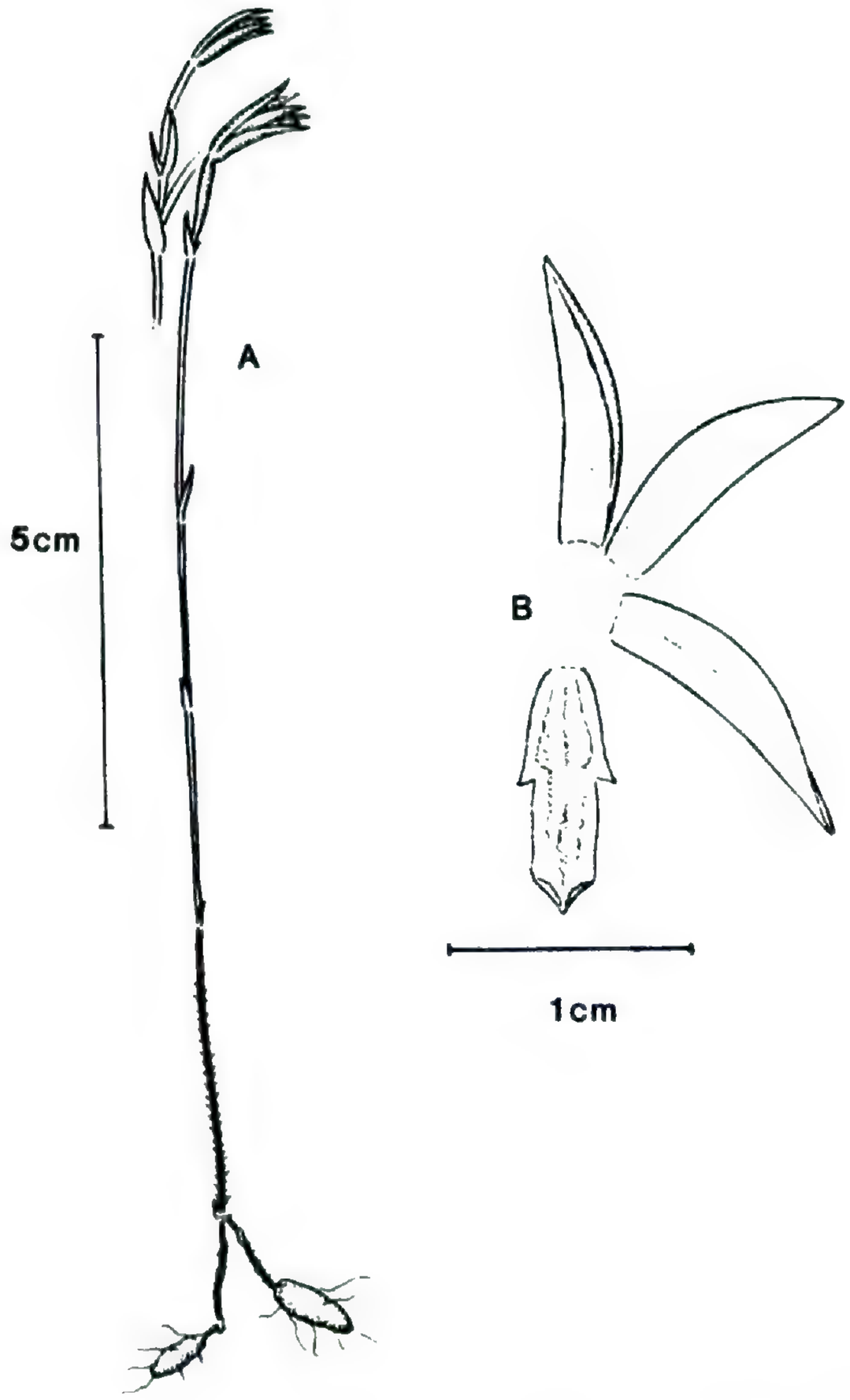


FIGURE 1. A, B. *Cleistes huberi* Carnevali & I. Ramírez.—A. Flowering habit.—B. Spread floral parts.

or slightly flexuous, glabrous, fistulose, internodes 3–35 mm long, clothed by strongly fused leaf sheaths. Leaves 4–7 mm long, 1.5–2 mm wide, reduced to small, fleshy, elliptic, acute, sheathlike blades, concave above, rounded below, margins finely erose. Inflorescences terminal, 1–2(–3)-flowered, flowers produced in succession. Floral bracts 2–5 mm long, similar to leaves but smaller. Flowers small for the genus, pale yellow to whitish, with subparallel perianth segments. Pedicellate ovary 7–10 mm long, subcylindric or narrowly ellipsoid, 6-ribbed. Sepals oblong-elliptic, acute, concave, 5-nerved, lateral sepals obliquely falcate; dorsal sepal 12–14 mm long, 2.2–2.5 mm wide, lateral sepals 11–13 mm long, 2.8–3 mm wide, dorsally carinate. Petals 10–12 mm long, 2.2–2.5 mm wide, linear-subfalcate, less concave than sepals, 3-nerved. Labellum 10 mm long, 3.5–4 mm wide, provided at base with 2 pedunculate, 0.2–0.3 mm long, subglobose calli, in outline narrowly oblong-ovate, 3-lobed about the middle; terminal lobe 5.5 mm long, 3.5–4 mm wide, linear-oblong to triangular-oblong, rounded or obtuse at apex, margins undulate, erect, making the blade concave; lateral lobes very small, 0.5 mm long and wide, toothlike, acute, porrect; disc with a pair of longitudinal, elevated, oblong, tuberculate callosities, the callosity longitudinally sulcate in middle, highest toward the base, apically extended into 3 tuberculate carinae occupying the terminal lobe. Column 4.5–5 mm long, basally attenuate; clinandrium wide with 4 teeth about 1 mm long. Anther subquadrate, with 1.5-mm-long projections. Rostellum obtriangular. Capsule 15 mm long, obovoid, olive green.

Paratypes. VENEZUELA. BOLÍVAR: Distrito Roscio, cumbre del Yuruaní-tepui, al NNW del Cerro Kukenán, vegetación herbáceo-arbustiva sobre planicies de arenisca en el sector centro-este del tepui, 2,300 m, 5°19′N, 60°51′W, 27 abril 1984, *O. Huber 9432* (VEN); Kukenán-tepui, cumbre del sector mas septentrional, algo separado del macizo principal, vegetación herbáceo-arbustiva sobre rocas de arenisca abiertas y alrededor de las lagunas, 2,500 m, 5°61′N, 60°48′W, 28 abril 1984, *O. Huber 9461* (NY, VEN); summit of Cerro Roraima, parte noreste, inmediata al sur del hito que marca los límites de Guyana, Brazil y Venezuela, 2,750–2,800 m, 5°12′N, 60°42′W, 26 agosto–2 septiembre 1976, *J. A. Steyermark et al. 112604* (VEN); cumbre del Tramén-tepui, en la porción mas nor-occidental del Macizo de Ilú-(Urú) tepui, 2,650 m, 5°27′N, 61°1′W, 23 enero 1985 (fr), *O. Huber 10062* (MFY, NY, VEN).

Etymology. After Otto Huber, who has collected this new species on several occasions.

Cleistes huberi is closely related to *C. stricta* (C. Schweinf.) Garay & Dunsterv., also from the Roraima Formation Tepui Area, from which it differs in its smaller size and by the lobation of the labellum, which is variable in its development. The degree of lobation correlates with the shape of the terminal lobe. Pronounced lobing is associated with an oblong terminal lobe, while a triangular terminal lobe is correlated with less conspicuous lobation. Plants of *C. huberi* are 4–15 cm high (usually under 10 cm high) and 1–2(–3)-flowered, while plants of *C. stricta* are 23–100 cm high and are much more floriferous, producing 2–7 flowers on a longer rachis. The flowers of *C. huberi* have sepals 11–14 mm long versus sepals 18–20 mm long in *C. stricta*. *Cleistes paludosa* Reichb. f. from Surinam and northern Brazil is similar but has larger leaves (1–2.5 cm long), the floral bracts are longer than the pedicellate ovary, and the perianth segments are longer and differently proportioned (sepals 18–19 mm long, 2–2.5 mm wide; labellum 15–16 mm long, 6–8 mm wide); *Cleistes aphylla* (Barb. Rodr.) Hoehne from southern Brazil (Paraná) is apparently related but plants are larger (up to 25 cm high), flowers are white, and the perianth segments are wider.

Cleistes stricta and *C. huberi* have distinct dis-

tributional patterns: *C. stricta* tends to be more common in the cerros or tepuis of Territorio Federal Amazonas, while *C. huberi* is restricted to the northeastern part of the Roraima Formation in Estado Bolívar. Their ranges slightly overlap, however, in Chimantá-tepui, which is the northernmost known location of *C. stricta*.

A recent field trip uncovered an unknown form of the common *Cleistes rosea* Lindley.

Cleistes rosea Lindley forma **pallida** Carnevali & I. Ramírez, forma nova. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Átures, morichal 1–2 km E de Piedra Tortuga, unos 8 km S de Puerto Ayacucho, 80–90 m, 30 junio 1988, ca. 5°32′N, 67°32′W, *G. Carnevali, I. Ramírez & G. A. Romero 2661* (holotype, VEN; isotypes, AMES, INPA, MO, MY, PORT, TFAV).

A *Cleistes rosea* Lindley forma *rosea* perigoniis angustioribus, pallide viridis, apice roseis vel purpureo striatis differt.

This new form has narrower sepals, petals, and labellum than the typical *C. rosea*; its flowers are held in a more nodding position, and it is particularly noteworthy by its color. While in the typical form all perianth segments are basically rose, pink, or purple, with darker zones in the labellum, in this new form the sepals are greenish cream, the petals are white, and the labellum is white with apical pink suffusion, with nerves that are apically dull purple. The callus is deep yellow as in the typical form. Populations of this form seem to be restricted to the northern part of Venezuelan Territorio Federal Amazonas, always at low elevations, and in *Trachypogon* savannas or at the ecotone between these savannas and "morichales" or forests.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Depto. Atabapo, sabana ubicada en el pie oriental del Cerro Cucurito en la ribera izquierda (Sur) del Medio Caño Yagua, 120 m, 3°36′N, 66°34′W, 28 junio 1979, *O. Huber 3872* (MYF, VEN); Depto. Atures, sabanas y bosques en la región de Rincones de Chacorro, unos 30 km N de Pto. Ayacucho, unos 5 km al NE de Galipero, 80 m, 5°48′N, 67°20′W, 9 mayo 1980, *O. Huber 5240* (MFY, VEN).

Our recognition of *Cleistes* Lindley as a distinct genus requires the following new combination.

Cleistes unifoliata (C. Schweinf.) Carnevali & I. Ramírez, comb. nov. BASIONYM: *Pogonia unifoliata* C. Schweinf., Fieldiana, Bot. 28: 171, fig. 27. 1951. TYPE: Venezuela. Bolívar: Ptari-tepui, scrubby forest on rocky open portion of plateau on SE-facing slopes, 1,600 m, 1 Nov. 1944, *J. A. Steyermark 59630* (holotype, F).

This rare species, previously known only from the type specimen and from recent material from Suriname (Werkhoven, 1986), has lately been collected several times in the Venezuelan Guayana, always on the Estado Bolívar tepuis, at 950–1,500 m.

Additional specimens examined. VENEZUELA. BOLÍVAR: Aparamán-tepui, 950 m, septiembre 1986, *A. Fernández 3580* (MFY, VEN); Amarway-tepui, 1,030 m, 5°55′N, 62°15′W, 27 mayo 1986, *Liesner et al. 21149* (MO, VEN); Cerro Guanacoco, cumbre, porción nor-oeste cerca del borde riscoso, sabana rodeada por bosque enano, 1,450 m, 4°46′N, 63°55′W, *Steyermark et al. 109724* (VEN); Cerro Sarisariñama, cumbre, porción E, afloramiento de arenisca con zanjones en formación de bosque achaparrado y árboles enanos, 1,380 m, 4°41′N, 64°13′W, *Steyermark et al. 108961* (VEN).

Subtribe Pleurothallidinae

This group, composed of about 4,000 species widely ranging through the Neotropics, is the largest assemblage of taxa at the subtribal level in the Orchidaceae. The systematics of the Pleurothallidinae have been recently reviewed by Luer (1986a) and we follow here the generic concepts he proposed. This subtribe comprises about 170 species in 16 genera in the Venezuelan Guayana; the largest genera are *Pleurothallis* (ca. 55 species), *Octomeria* (ca. 30 species), and *Stelis* (ca. 18 species). Here we propose as new three ecologically similar species.

Octomeria romerorum Carnevali & I. Ramírez, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Átures, carretera a Gavilán, ca. 3 km antes del puente sobre el Río Gavilán, julio 1987, *G. A. Romero, F. Guánchez & E. Gutiérrez 1324* (holotype, VEN; isotypes, K, MO, TFAV). Figure 2A–D.

Species *Octomeria gemmulae* Carnevali & I. Ramírez similis sed statura vegetativa manifeste minore, folio quam ramicaulo conspicue breviore et labello anchoriformi differt.

Diminutive, creeping, epiphytic herbs, forming clumps 3–8(–15) cm long and wide, adpressed to bark. Rhizome ca. 1 mm thick, bearing ramicauls 0.5–1 mm apart, concealed by scarious sheaths. Ramicauls 1–2 mm long, 0.6–0.8 mm thick toward apex, monophyllous, abbreviated, shorter than leaves, obconic to subcylindric, 1-articulated, suberect to horizontal, concealed by scarious sheaths.

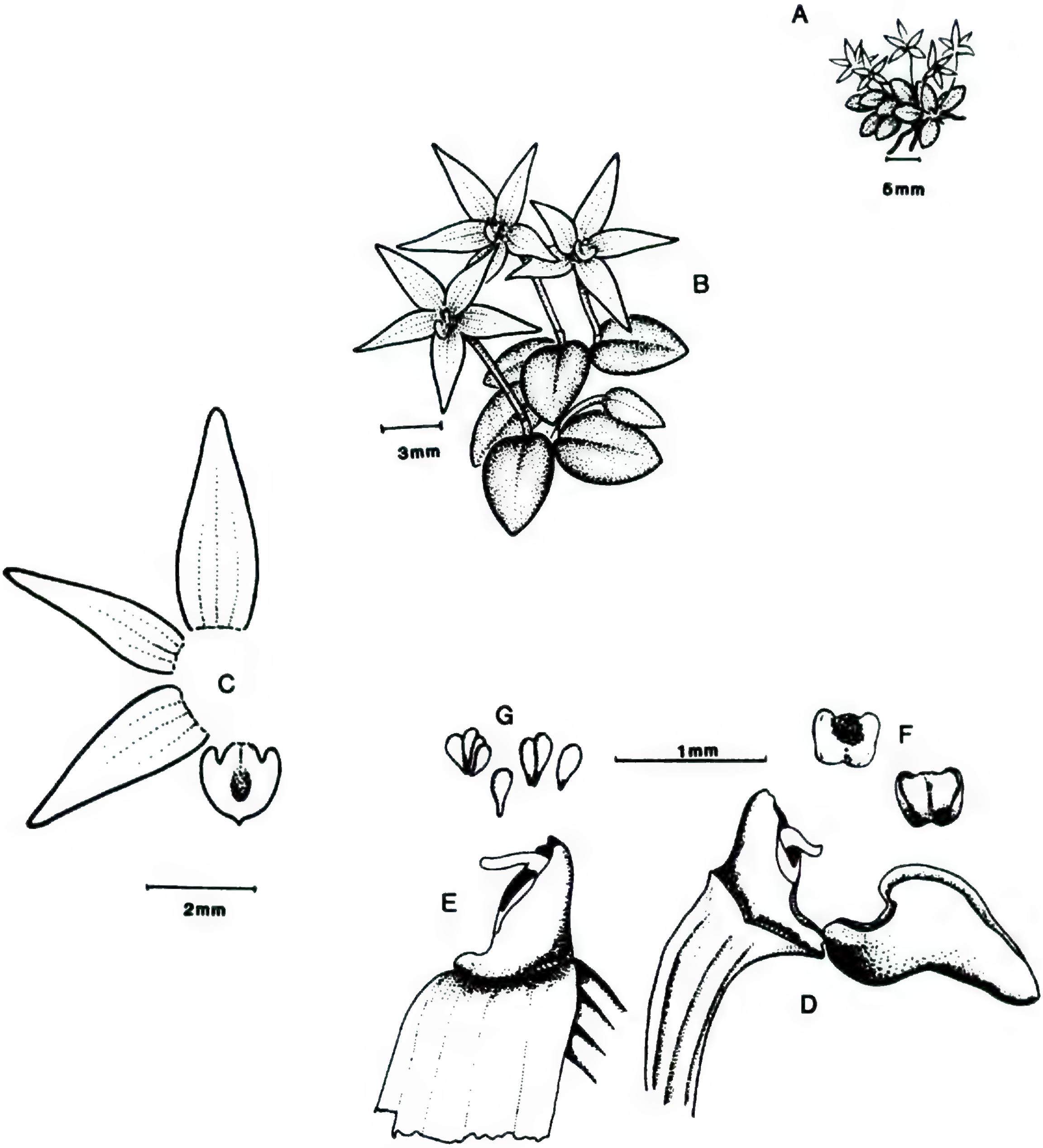


FIGURE 2. A–G. *Octomeria romerorum* Carnevali & I. Ramírez.—A, B. Flowering habit.—C. Perianth segments, flattened.—D. Lateral view of labellum and column.—E. Lateral view of column, showing rostellum.—F. Anther, ventral and dorsal view.—G. Pollinia.

Leaves 5–6(–7) mm long, 3.2–3.8 mm wide, fleshy coriaceous, thick, adpressed to the substrate, green, concolorous, elliptic to widely elliptic, apex usually obtuse but ranging from subacute to rounded, base rounded to obtuse, abaxially flat or somewhat convex with a flat to sulcate midrib, abaxially convex; the margins rounded. Inflorescences 1-flowered, successive, erect, originating from a mass of sheaths, peduncle 1.5–2.8 mm long, subterete, 1-articulate, clothed with tubulose, scarious sheaths. Floral bracts rudimentary. Pedicellate ovary 4–5 mm long. Pedicel 3–4 mm long, thin, subterete. Ovary 0.8–1.2 mm long, straight or in angle with pedicel, somewhat hexasulcate. Flowers large for the plant, white-hyalinous, opening well with flat or somewhat recurved-reflexed perianth segments. Perianth segments membranaceous, subequal, 3-nerved. Sepals 3–4 mm long, 0.8–1.2 mm wide, free, narrowly

elliptic to narrowly ovate-elliptic, acute, the lateral sepals slightly oblique. Petals 3–4 mm long and ca. 1 mm wide, narrowly ovate-elliptic, acuminate, apically somewhat concave. Labellum 1.2–1.3 mm long and 1.1–1.3 mm wide, fleshier than the other perianth segments, concave, from a cuneate claw cordate-suborbicular to cordate-broadly ovate, acute, minutely apiculate; the claw 0.2–0.3 mm long; the blade 3-lobate, basal lobes 0.2 mm long, subfalcate-triangular, obtuse, rounded, to subacute, retrorse, thus making an anchiroid labellum; disc provided with a longitudinally elliptic, pulvinate callus. Column 0.5–0.6 mm long, short and thick, foot ca. 3 mm long. Rostellum 0.15–0.2 mm long, linguiform. Pollinia 8.

Etymology. This species is named after Gustavo and Peggy Romero, who first collected it.

This description was compiled from live and liquid-preserved material from the type collection. This species seems to be near to *Octomeria gemmula* Carnevali & I. Ramírez from the Río Sipapo drainage, with which it shares the small creeping habit (but not strongly "*Peperomia*-like" in *O. gemmula*, see discussion below), thick leaves, long-peduncled and proportionately large white flowers, and more or less similar labella. In both species the flowers open at about 7:00 A.M. and close at about 1:00 P.M. for 3–6 days. *Octomeria gemmula*, however, differs by its larger habit with proportionately longer ramicauls, purplish abaxial face of the leaves, and antrorse lateral lobes of the labellum. *Octomeria romerorum* seems to be restricted to dense forests where it grows on high branches, while *O. gemmula* grows low on shrubs in sandy, open scrublands.

Octomeria romerorum seems unique in the genus because of its habit, which recalls some of the species of *Pleurothallis* subg. *Specklinia* sect. *Muscosae* (Luer, 1986b) and a few species of *Platystele* Schltr. All these species have very short ramicauls along a short- to long-creeping rhizome with thick prostrate leaves forming small masses over the surface of the host tree. In habit they resemble some of the species of *Peperomia* in the *P. rotundifolia* (L.) HBK complex. It is interesting to note that in northern Territorio Federal Amazonas and in adjoining Distrito Cedeño of Edo. Bolívar, there are several species of Pleurothallidinae that share the same "*Peperomia*-like" habit and that grow more or less sympatrically, namely: *Pleurothallis pemonum* Carnevali & I. Ramírez, *P. deborana* Carnevali & I. Ramírez, *P. nanifolia* Fold., *Platystele ovalifolia* (Focke) Garay & Dunsterv., and this new species. This is an area of heavy rainfall but with a marked dry season between December and March. It is quite probable that this "*Peperomia*-like" habit minimizes water loss because the stomata-bearing abaxial leaf surface is closely adpressed against the substrate, creating a closed, humid atmosphere.

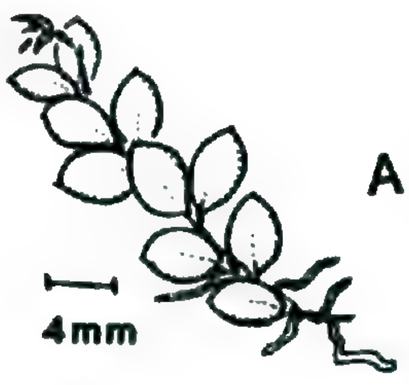
Octomeria romerorum does not fit in any of the proposed subsections of sect. *Octomeria* (Cogniaux, 1896; Luer, 1986a). Its small vegetative stature would include it in subsect. *Pusillae* but its free lateral sepals would place it in subsect. *Octomeria*. The current classification of *Octomeria* appears artificial and a new intrageneric classification is needed.

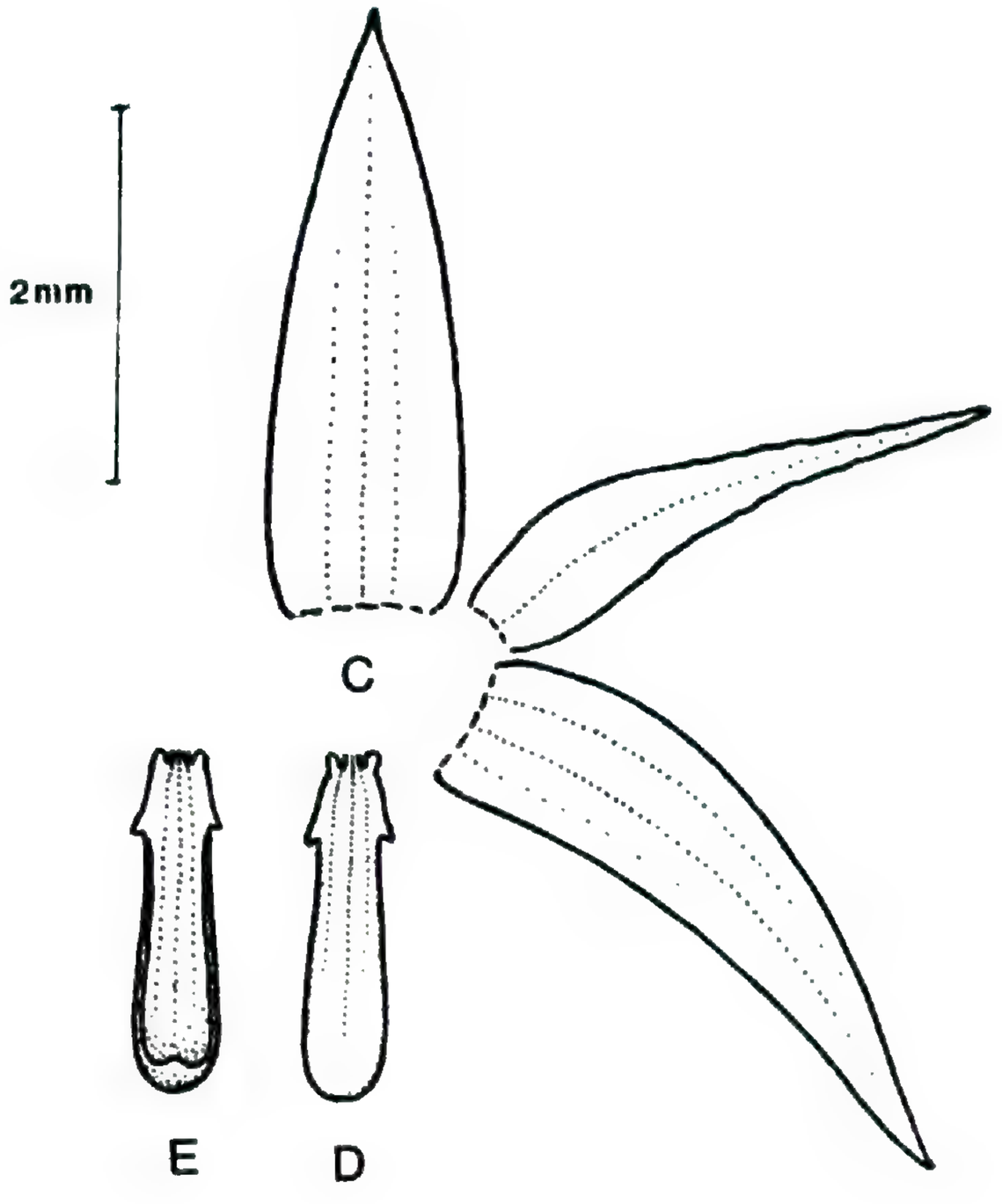
Two small, creeping species of *Pleurothallis* of the affinity of *P. nanifolia* Fold. have been found in the northern Venezuelan Guayana which have proved to be new to science.

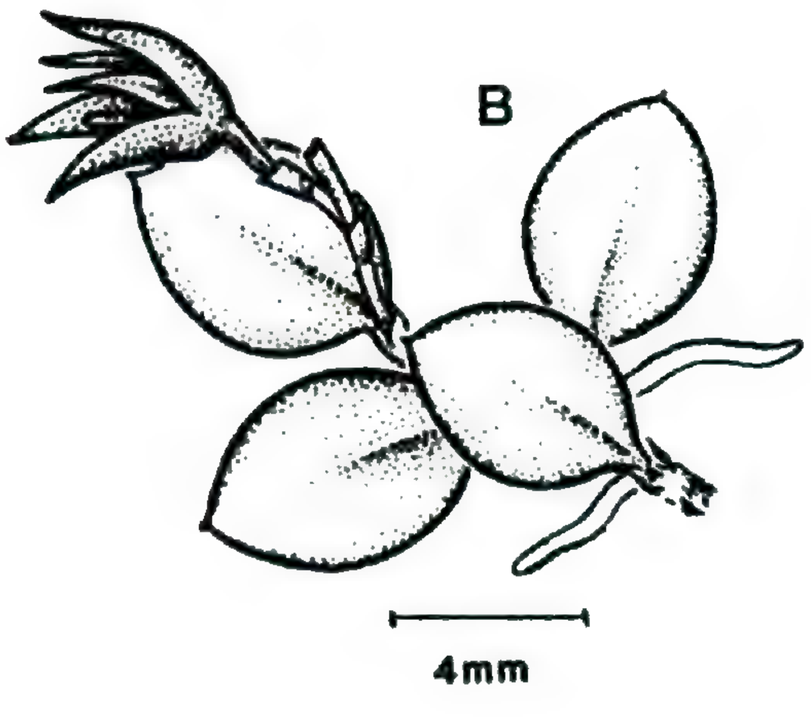
Pleurothallis deborana Carnevali & I. Ramírez, sp. nov. TYPE: Venezuela. Bolívar: Distrito Cedeño, bosque al borde de sabana al E del Río Parguaza, 125 km al N de Pto. Ayacucho, ca. 100 m, originalmente colectada por Bruce Holst y florecida en el vivero de los colectores, junio 1987, *G. Carnevali & I. Ramírez 2317* (holotype, VEN). Figure 3D, E.

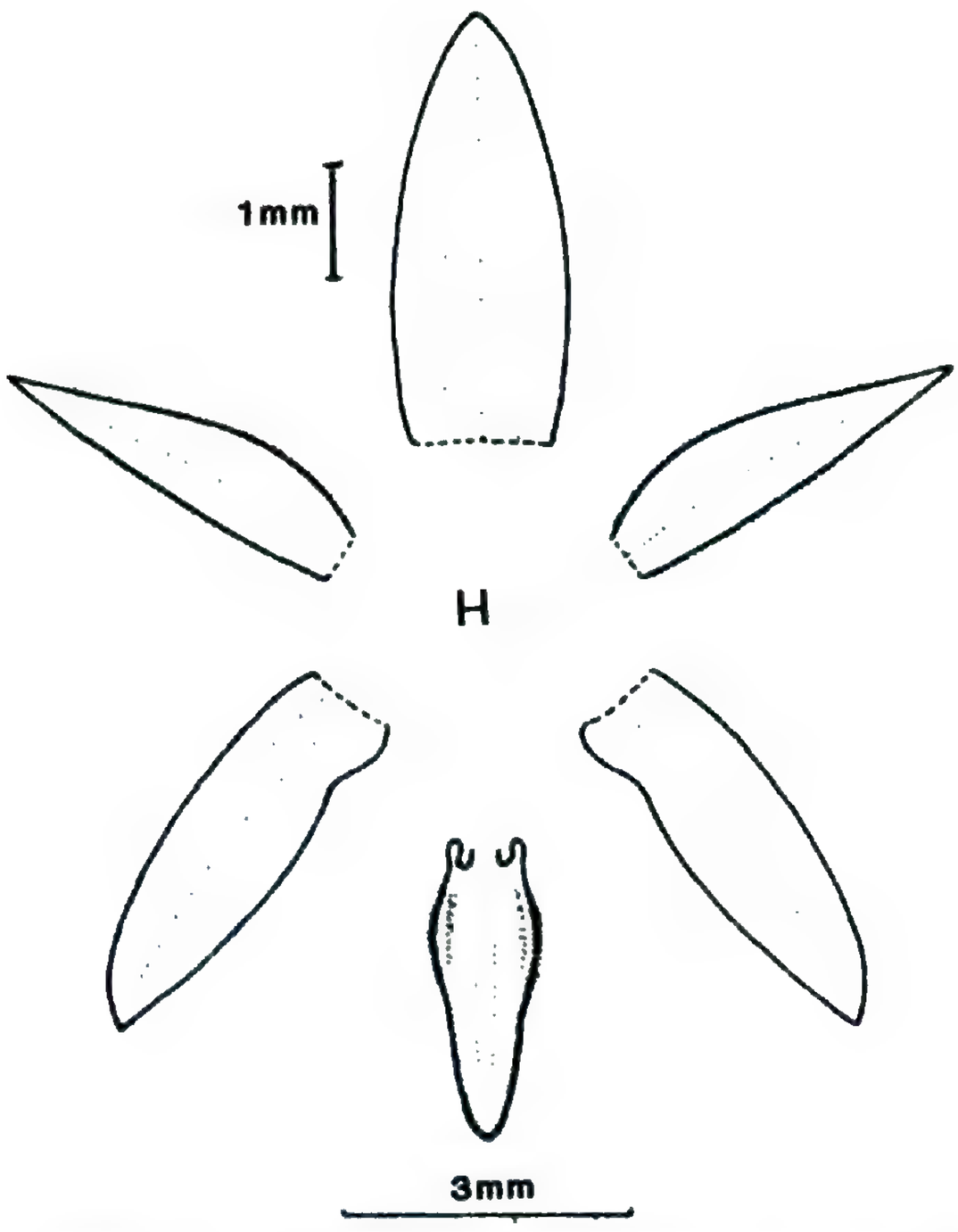
Species *Pleurothallis nanifoliae* Fold. affinis, sed petalis ellipticis, acuminatis et labello anguste-obovato, apice rotundato, recurvato recedit (subg. *Specklinia*, sect. *Muscosae*).

Small, creeping epiphytes, adpressed to substrate, 2–6 cm long. Rhizome 1 mm thick, creeping, concealed by scarious sheaths, adult ramicauls 1–3 mm distant. Ramicauls 1–2 mm long and about 1 mm thick, subterete, apically thickened. Leaves 5.5–8 mm long, 4.5–6.5 mm wide, fleshy coriaceous, flat, prostrate over the substrate, broadly elliptic to (rarely) broadly ovate, obtuse, apiculate, base broadly cuneate. Inflorescences 1–2 originating from the ramicaul apex, racemes 1–3-flowered, erect, shorter than subtending leaves, provided with a tubulose, apiculate sheath. Rachis slightly flexuose, subterete. Floral bracts 1 mm long, applicate, apiculate, green. Pedicel 2–2.3 mm long, subterete, somewhat thickened apically, green tinged with red-purple. Ovary triquetrous, basally attenuate, 0.8 mm long, green with purple markings. Flowers resupinate, subcampanulate, small but large for plant size. Perianth segments subfleshy. Sepals 3.2 mm long, 0.8–1 mm wide, somewhat concave, clear greenish yellow, maroon-tinged within, narrowly ovate-lanceolate; lateral sepals slightly connate basally, somewhat falcate, dorsally carinate. Petals 3 mm long, 0.7 mm wide,









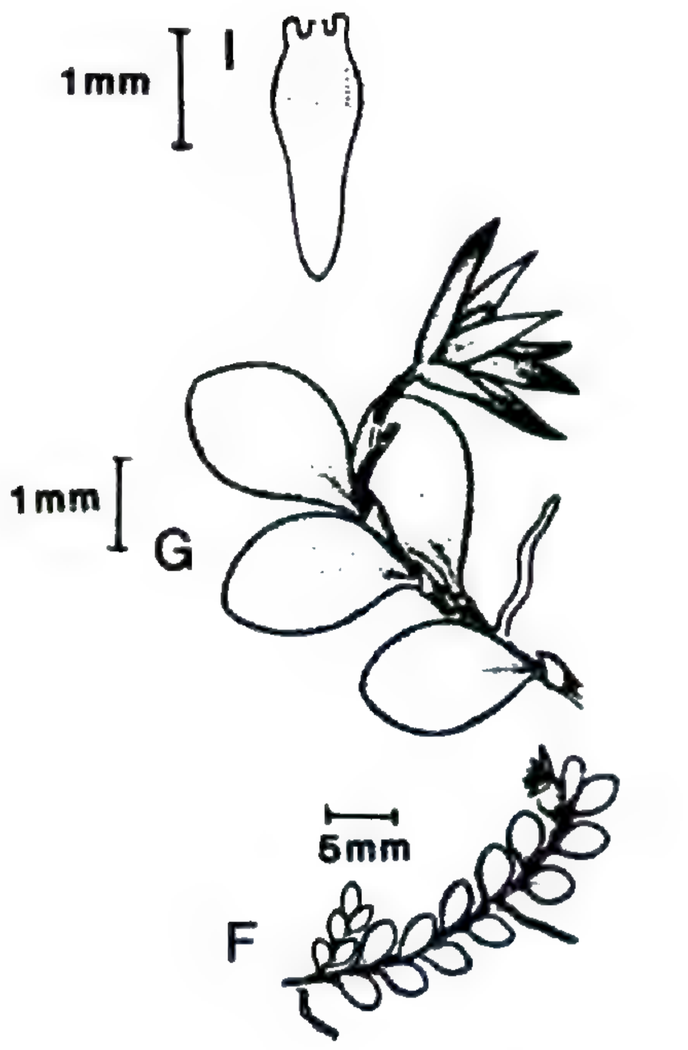


FIGURE 3. A–E. *Pleurothallis deborana* Carnevali & I. Ramírez.—A, B. Flowering habit.—C. Perianth segments, flattened.—D. Labellum, ventral view.—E. Labellum, dorsal view. F–I. *Pleurothallis pemonum* Carnevali & I. Ramírez.—F, G. Flowering habit.—H. Perianth segments, flattened.—I. Labellum, flattened. H redrawn from an original tracing by G. C. K. Dunsterville.

with the general coloration of the sepals but with a dark purple longitudinal central zone, narrowly ovate-lanceolate, acuminate, slightly falcate, margins finely erose toward apex. Labellum 1.8 mm long, 0.4 mm wide, fleshier than the other perianth segments, dark red-purple with a yellow longitudinal streak, the ventral surface finely papillose, narrowly oblong-obovate, apex recurved and acute beneath, the ventral face provided with a longitudinal concavity, margins carinate, at the basal ¼ provided with 2 small lobes 0.3–0.4 mm long, these somewhat falcate, acute; labellar base provided with two small auricles. Column 1.6 mm long, relatively slender, arcuate, alate in the apical half, clinandrium trilobed, 0.8–0.9 mm wide when expanded. Anther smooth, subglobose. Pollinia 2.

Etymology. After Debora, our daughter.

This description was prepared from living material from the only plant known. It was collected in the same tree where *Pleurothallis holstii* Carnevali & I. Ramírez was originally found. The only flower is preserved as the holotype.

Pleurothallis deborana shares the same general habit and similar flowers with *P. nanifolia*, *P. pemonum* Carnevali & I. Ramírez, *P. pachyphyta* Luer, and other species of *Pleurothallis* subg. *Specklinia* sect. *Muscosae*. Perhaps its closest ally is *P. pemonum*, which has identical habit and petals. However, *P. deborana* differs by its narrowly obovate labellum (vs. ovate-lanceolate) of smaller size (1.8 mm long vs. 2.5–3.2 mm long in *P. pemonum*), with a rounded, recurved apex (vs. not recurved). Both are easily differentiated from *P. nanifolia* by their apically attenuate petals (vs. obovate).

Pleurothallis pemonum Carnevali & I. Ramírez, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Átures, carretera a Gavilán, sobre *Parkia pendula*, ca. 5 km al E del Fundo Doña Juana, asociada con *Octomeria romerorum*, julio 1987, *G. A. Romero 1334* (holotype, VEN; isotype, TFAV). Figure 3F–I.

Species *Pleurothallis nanifoliae* Fold. affinis, sed petalis ellipticis, acutis et labello subsimplici differt (subg. *Specklinia*, sect. *Muscosae*).

Small, creeping epiphytes up to 2 cm high. Rhizome 0.6–0.8 mm thick, subscandent, entirely concealed by scarious sheaths, bearing 1–2 relatively thick roots at each node. Ramicauls 1–3 mm long, 1–2 mm apart on the rhizome, subterete, noticeably thickened apically, concealed by tubular, scarious sheaths, apically monophyllous. Leaves 5–7(–9) mm long, 3–5 mm wide, very fleshy, usually adpressed to the host's bark but occasionally suberect, usually broadly elliptic or broadly obovate-elliptic, rarely elliptic to almost orbicular, apex obtuse to rounded, with a subapical mucro, base obtuse to rounded. Inflorescence 4–7 mm long, erect, originating from the leaf base, racemose, 1–2-flowered, basally enclosed by scarious sheaths. Floral bracts 0.8 mm long, ovate-elliptic, acute, acuminate, slightly scabrous. Pedicel subterete, 1.5–1.8 mm long. Ovary 0.6–0.8 mm long, obconic, subtriquetrous, in angle to pedicel. Flowers proportionately large, lateral sepals patent, dorsal sepal, petals, and lip parallel to labellum. Perianth segments subcoriaceous. Sepals trinerved; dorsal sepal 3.8–4 mm long, 0.8–1 mm wide, narrowly oblong, acute; lateral sepals 3.2–3.5 mm long, 1–1.2 mm wide, linear oblong, acute, slightly oblique, free to their bases where they form a shallow mentum. Petals 2.8–3.7 mm long, 0.8–0.9 mm wide, margins microscopically cellular. Labellum 2–2.2 mm long, 0.5–0.6 mm wide, parallel to the column, fleshier than the other perianth segments, narrowly ovate-lanceolate, apex acute to subobtuse, basally provided with a pair of small, rounded, 0.2 mm long lobules or auricles, ventral face provided with a dense, minute pubescence absent along a longitudinal concavity extending to the apex of the blade. Column 1.8–2 mm long, slightly arcuate, subterete, apically winged and trilobed; clinandrium fimbriate. Anther subventral.

Paratypes. VENEZUELA. BOLÍVAR: selva virgen siempre verde a lo largo de la Quebrada Los Brasileros, 4.5 km al S de Icabarú, 4°20′N, 61°48′W, 480 m, diciembre 1976, *Steyermark et al. 117784* (VEN); Río Carrao, 450 m, *Dunsterville & Dunsterville 1221* (AMES, VEN).

Etymology. After the Pemón Indies from La Gran Sabana, Edo. Bolívar, who live where this species occurs.

This small, creeping species is closely related to *Pleurothallis nanifolia* and *P. deborana*. (See discussion under the latter species.) The flowers of *P. pemonum* have semitranslucid, deep wine-red sepals, petals of the same hue but not translucid; the labellum is dark red with the central concavity yellow-cream, basally grandular-pubescent. The column is cream, red-tinged dorsally, ventrally dark red. The anther is creamy red, the ovary is yellow and the pedicel is creamy red.

Pleurothallis pemonum has a wide range in the Venezuelan Guayana and with little doubt is present in Brazil and Colombia. The Dunstervilles collected it in several places in Edo. Bolívar: Río Carrao, 450 m, and Cerro Guaiquinima, 700 m (G. C. K.

Dunsterville, pers. comm.). The authors have found it in the Akaruai River at 750 m (no voucher), in the same state. The holotype collection is somewhat out of range but otherwise is identical.

We agree with Luer (1986a) that the kind of stigma structure (1-lobed, ventral) found in *Apatostelis* (as defined by Garay, 1980) is only an extreme case in a rather variable character and should not be used as a generic criterion. Hence, the following combination is required:

Stelis garayi (Dunsterv.) Carnevali & I. Ramírez, comb. nov. BASIONYM: *Apatostelis garayi* Dunsterv., Amer. Orchid Soc. Bull. 50: 1075. 1981. TYPE: Venezuela. Bolívar: Salto Paraván, Río Yuruán, ca. 250 m, *G. C. K. Dunsterville 1418* (holotype, AMES; isotype, VEN).

This interesting little species, related to a group of mainly Central American species (*Stelis ciliaris* Lindley, *S. crescenticola* Schltr., *S. minimiflora* Schltr., and others), has recently been collected again, now in the Venezuelan Amazonas. The specimen is: Venezuela. Territorio Federal Amazonas: Depto. Atures, Río Autana, 200 m, enero 1988, *G. A. Romero 1435* (TFAV, VEN).

SOBRALIA

The genus *Sobralia* Ruíz Lopez & Pavón, containing about 80 species, is mainly a Middle American and Andean genus. However, a secondary center of diversity is to be found in the Guayanan Highlands; most of the species occurring there are endemics to that area. The flowers of plants belonging to this genus are very difficult to study since they are thinly membranous and tend to agglutinate. Because of this problem, many species are ill-defined or poorly known and the genus is in need of a revision. There are 19–20 species of *Sobralia* in Venezuela, most of them restricted either to the Andean portion of the country or to the Guayana, where 13 species are known to occur. One of them is proposed as new here.

Sobralia oliva-estevae Carnevali & I. Ramírez, sp. nov. TYPE: Venezuela. Estado Bolívar: Parque Nacional Canaima, La Escalera, bosque nublado enano alrededor del km 125 al S de El Dorado, ca. 1,300 m, 30 agosto–8 septiembre 1987, *I. Ramírez, G. Carnevali & F. Oliva-Esteva 150* (holotype, VEN). Figure 4.

Species *Sobralia speciosae* C. Schweinf. similis, sed caules ramificantes, subscandentes (vs. simples); folia abaxialia 2-carinata (vs. 3–5-carinata), inflorescentia semper uniflora (vs. (2–)3–5-flora), petala apice non undulata (vs. undulata) recedit.

Medium-sized to rather large epiphytic to subterrestrial, suffruticose herbs. Roots thick. Stems 100–250 cm long, terete, erect, arcuately ascendent to subpendulous, sometimes red-tinged, somewhat lignified basally, branching and rooting at the upper half, basal internodes 18–25 cm long, nodes somewhat thickened, apical internodes and branches 1–8 cm long, leafy. Leaves 5–10.5 cm long, 1–1.9 cm wide, subfleshy when fresh, rigidly coriaceous when dry, abaxially with 2 raised nerves, decurved in natural position, narrowly ovate-elliptic to ovate-elliptic, long acuminate, articulate with their sheaths; sheaths 0.5–1.2 cm long, tightly clasping the stem. Inflorescences uniflorous, axillary from the upper portion of main stem or branches, up to 6 flowers per branch; peduncle 20–30 mm long, somewhat ancipital and apically thickened, its basal half enveloped by the subtending leaf sheath, apically produced into a fugacious aborted flower, noticeable only on fresh material. Pedicellate ovary 1.4–1.5 cm long, subterete, twisted. Flowers 9–12 cm natural spread, showy, resupinate, with submembranaceous, widely spreading perianth segments, lasting only one day. Sepals and petals purple, paler toward apex. Dorsal sepal 5 cm long, 1.8 cm wide, narrowly obovate-elliptic, subacute. Lateral sepals 5.2 cm long, 1.7 cm wide, elliptic, acute. Petals 5.3 cm long, 2.3 cm wide, obovate, abruptly acute, somewhat incurved in natural position. Labellum 5.7 cm long, 4.4 cm wide, rich purple with a white throat and a yellow central carina, this reaching only the opening of the throat, hairs on disc pale purple, in outline broadly obovate-elliptic or somewhat rhomboid, broadly rounded apically, emarginate and mucronulate, labellar margin undulate-crisped in the apical half, disc with 4 hairlike antrorse to suberect lamellae-covered carinae at each side of central nerve, this bearing lamellae at the apical third. Column 2.8 cm long, 4.5–5 mm thick, slender, somewhat clavate, apically triquetrous, clinandrium trilobate, central lobe larger than laterals.

Paratypes. GUYANA: Kaieteur Plateau, 11 May 1944, *Maguire & Fanshawe 23380* (AMES, NY). VENEZUELA. BOLÍVAR: Uei-tepui, between southeastern slope and summit, between Luepa and Cerro Venamo, vicinity of km 125 S of El Dorado, 1,100–1,300 m, Mar. 1962, *Steyermark & Aristeguieta 21* (VEN).

Etymology. After Francisco Oliva-Esteva, who participated in the collection of the type specimen.

This description was based on pickled material

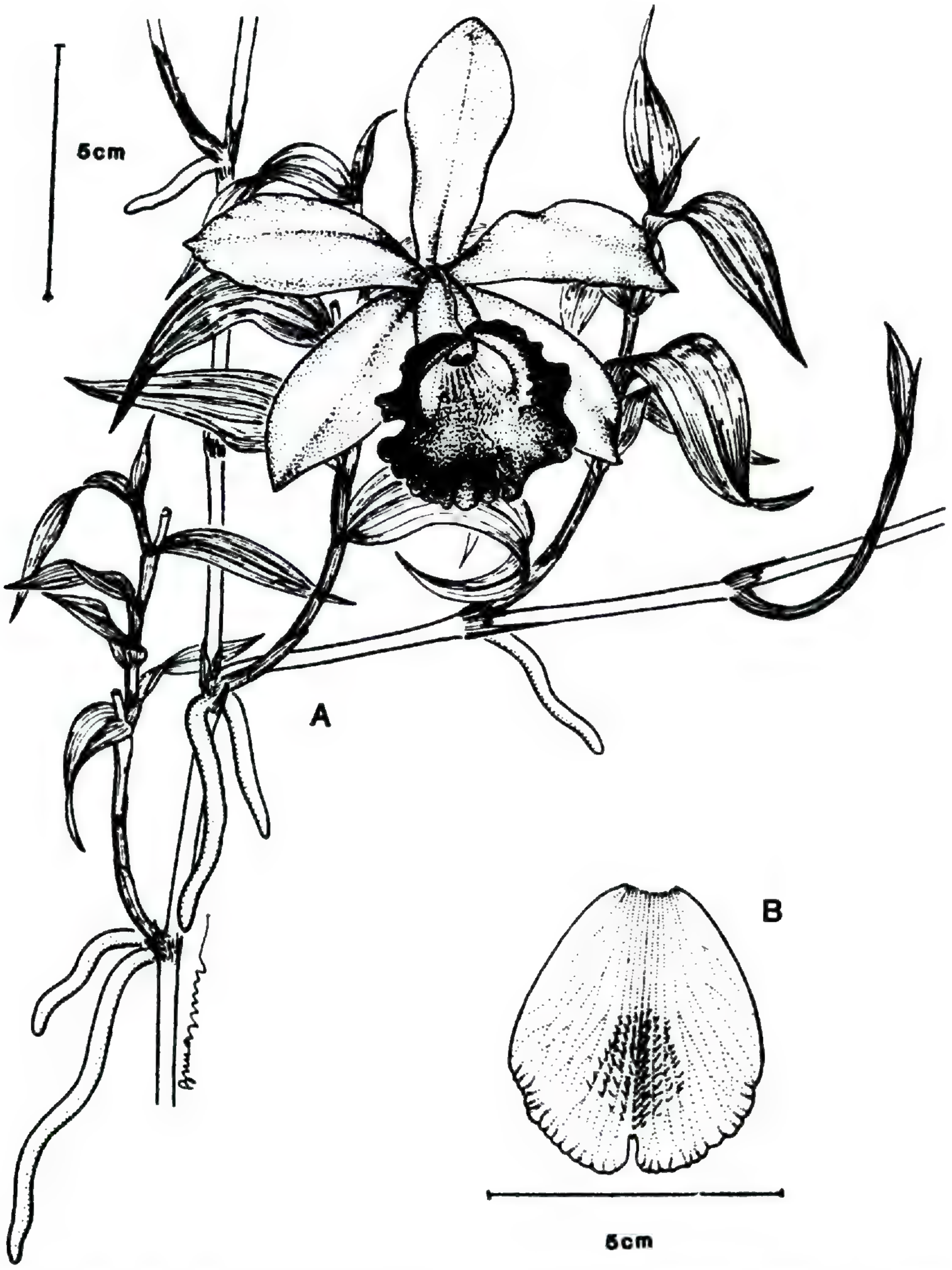


FIGURE 4. A, B. *Sobralia oliva-estevae* Carnevali & I. Ramírez.—A. Flowering habit.—B. Labellum, flattened.

from the holotype collection and on dried material from the paratypes.

The flowers of this showy species are almost identical to those of *Sobralia speciosa* C. Schweinf. from southern Territorio Federal Amazonas (Cerros Neblina, Avispa, and Aracamuni), but in *S. oliva-estevae* the petals are marginally flat, and the labellum is more obovate and proportionally wider. The pedicellate ovary in *S. speciosa* is proportionally longer than in *S. oliva-estevae*; in the first species it is 0.75–1.3 times longer than the column (p. ovary 2–4.7 cm, column 3–3.5 cm), while in the new species the pedicellate ovary is only about half as long as the column (p. ovary 1.4–1.5 cm, column 2.8 cm). The most striking differences between both species, however, lie in the vegetative morphology and in their ecological preferences. *Sobralia speciosa* grows terrestrially in open savannalike tepui associations, usually in boggy conditions while *S. oliva-estevae* is an epiphyte in cloud forests. In *S. oliva-estevae* the stems are freely branching and proliferous in the upper half, rooting at the branching internodes; in this way the plants become subscandent, eventually prostrate or pendulous. The stems in *S. speciosa* are simple and erect. The leaves of *S. speciosa* have 3–5 nerves raised abaxially, while in *S. oliva-estevae* there are only 2. In *S. speciosa* the inflorescence is a suc-

cessively (2–)3–5-flowered raceme (rarely with 2 flowers open simultaneously), while in the new species the inflorescence is always 1-flowered; several axillary inflorescences are produced successively toward the apex of each stem or branch.

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POLLINATION ECOLOGY OF SEVEN SPECIES OF *BAUHINIA* L. (LEGUMINOSAE: CAESALPINIOIDEAE)[1]

Omaira Hokche[2] *and Nelson Ramirez*[2]

Abstract

Pollination and floral biology of seven species of *Bauhinia* were analyzed between 1982 and 1983 in different Venezuelan plant communities. *Bauhinia* species are grouped in two sections: *Pauletia*, which includes trees, and *Tylotaea*, which includes lianas. The species of sect. *Pauletia* included in this study (*B. aculeata*, *B. multinervia*, *B. pauletia*, *B. ungulata*) have comparatively large, white flowers, while the species of sect. *Tylotaea* (*B. glabra*, *B. guianensis*, *B. rutilans*) exhibit different colors of flowers and variations in form and color of the upper petal. Nectar analyses were made for six *Bauhinia* species for sugar and amino acid composition. The species of sect. *Tylotaea* produce less nectar with a higher sugar concentration than those of sect. *Pauletia*. Hexose is dominant in species of sect. *Pauletia* except in *Bauhinia aculeata*, where sucrose is dominant. The species of sect. *Tylotaea* have comparatively small diurnal flowers and are visited by a great variety of bees, wasps, butterflies, and hummingbirds; those of sect. *Pauletia* are mainly nocturnal and bat-pollinated, but *Bauhinia aculeata* showed different behavior and could be intermediate between the two sections. The flower morphology, floral biology, pollinator species, nectar composition, and secretion tend to be associated with the life form of the two sections of *Bauhinia*.

In an ecological context, caesalpinioid legume flowers are less specialized than their mimosoid and papilionoid counterparts. Caesalpinioid flowers are open, usually with exposed pollen and nectar available to specialized and nonspecialized pollen vectors. Only in some of the advanced genera are resource conservation and pollinator selection evident (Arroyo, 1981). The Caesalpinioideae exhibit a great variety of pollinating agents and mechanisms with an entomophilous trend (Arroyo, 1981). For example, many *Cassia* species are bee-pollinated (Delgado et al., 1977). In this sense, ornithophily and chiropterophily are scarce (Arroyo, 1981).

Studies of chiropterophily have paid comparatively more attention to the legumes of the New World than of the Old World (Frankie & Baker, 1974; Heithaus et al., 1974, 1975; Howell, 1975; Bernhardt, 1982; Ramirez et al., 1984; Prance, 1985). Some neotropical *Bauhinia* species are bat-pollinated (Heithaus et al., 1974; Ramirez et al., 1984). However, Vogel (1954) reported that *Bauhinia galpinii* and *B. mucronata* are sphingophilous, and Arroyo (1981) suggested that many other species of *Bauhinia* are probably sphingophilous.

The flowers of neotropical *Bauhinia* species exhibit great diversity in form, size, and color, which has been poorly studied from an adaptive viewpoint. The species of *Bauhinia* are grouped in three sections according to Stuard da Fonseca Vaz (1979). Section *Pauletia* comprises trees and shrubs; in contrast, species of sects. *Tylotaea* and *Schnella* comprise climbing plants. For all *Bauhinia* species studied, the flowering periods occur during the dry season.

The following study provides information about the floral biology and pollinator activity of seven species of *Bauhinia* belonging to sects. *Pauletia* and *Tylotaea* found in different plant communities of Venezuela. The chemical composition, secretion, and volume of the nectars produced were analyzed for comparing both sections of *Bauhinia*.

Dates and Methods

Bauhinia is widely distributed in several ecosystems in Venezuela. The localities for this study

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TABLE 1. Life form, reproductive phenology, and study sites of *Bauhinia* species.

Section Species	Life form	Flowering period	Fruiting period	Locality	Elevation (m)	Coordinate	Forest type[1]	Mean annual rainfall (mm)	Temperature (°C)
Pauletia									
B. aculeata	tree	Feb.–July	July–Nov.	Biological Reserve (Arboretum de la Escuela de Biología, Universidad Central de Venezuela), Colinas de Bello Monte, Caracas, Estado Miranda	1,100	10°30′N, 66°53′W	Dry Premontane Forest	550–1,100	18–24
				El Palmar village, 50 km NE of Upata, Estado Bolívar and 60 km of Imataca Forest Reserve	100	7°39′N, 66°07′W	Tropical Dry Forest	1,000–1,800	22–29
B. multinervia	tree	Nov. Jan.	Dec.–Mar.	Along the Caracas River, Los Caracas, Distrito Federal, Departamento Vargas	8	10°37′N, 66°34′W	Dry Premontane Forest	550–1,100	18–24
B. pauletia	tree	Sep.–Nov.	Oct.–Mar.	San Sebastián de Los Reyes, Estado Aragua	200	9°56′N, 67°10′W	Dry Premontane Forest	550–1,100	18–24
B. ungulata	tree	Nov.–Jan.	Dec.–Mar.	Estación Biologica de Los Llanos, Sociedad Venezolana de Ciencias Naturales, approximately 12 km SE of Calabozo, Estado Guárico	75	8°56′N, 67°25′W	Tropical Dry Forest	1,000–1,800	22–29
Tylotaea									
B. glabra	liana	Sep.–Feb.	Oct.–May	Biological Reserve (Arboretum de la Escuela de Biología, Universidad Central de Venezuela), Colinas de Bello Monte, Caracas, Estado Miranda	1,100	10°30′N, 66°53′W	Dry Premontane Forest	550–1,100	18–24

TABLE 1. Continued.

Section Species	Life form	Flowering period	Fruiting period	Locality	Elevation (m)	Coordinate	Forest type[1]	Mean annual rainfall (mm)	Temperature (°C)
B. guianensis	liana	Feb.–Apr.	Mar.–May	Imataca Forest Reserve in the Estación Experimental de Río Grande, Distrito Piar y Roscío (Estado Bolívar), and Territorio Delta Amacuro	266	8°03′N, 61°39′W	Humid Tropical Forest	1,800	24
B. rutilans	liana	Sep.–Oct.	Oct.–Mar.	Henry Pittier National Park, close to Rancho Grande Biological Station, Estado Aragua	1,100	10°21′N, 67°41′W	Very Humid Premontane Forest	2,000–4,000	18

[1] According to Ewel et al. (1976).

were chosen in accordance with the flowering and fruiting periods indicated on specimens in the Herbario Nacional de Venezuela (VEN) and through field observations (Table 1) in various regions.

Field observations were made of the life form and height of plants, and pollination and floral biology were analyzed in 1982–1983 during the flowering and fruiting periods of each species.

FLORAL CHARACTERISTICS

The floral parts (corolla, pistil, stigma, and petal lengths) were measured using samples preserved in 70% ethanol for 20 flowers from five to ten individual plants of each *Bauhinia* species.

FLORAL BIOLOGY

Flowers were observed in situ to record anthesis: inflorescences with buds about to open were marked before anthesis, and progress of anthesis was observed every 30 minutes. The pattern of nectar production was measured periodically with microcapillaries inserted in the hypanthium cavity of bagged flowers. Solute concentration of the nectar was measured with a manual Bausch & Lomb refractometer (range 0–30%). The presence of sugar, proteins, amino acids, lipids, and other compounds was detected from nectar on filter paper by Drs. Irene & Herbert Baker (University of California, Berkeley, California, U.S.A.). Pollinator activity was observed and recorded during five days for each *Bauhinia* species. The visiting agents observed were captured with hand nets and mist nets and were examined for pollen load.

RESULTS

FLORAL MORPHOLOGY

The inflorescences of *Bauhinia* are axillary and/or terminal. The sect. *Pauletia* species have comparatively large, white flowers; the stamens are dimorphic: five are large and five short (Table 2). However, this trend was not clear for all species of this section. In *Bauhinia pauletia* short stamens are represented by five staminodes. The flowers of short and long pistils were found on the same tree of *B. aculeata*. The short pistil flowers are not located in the inflorescence. In 100 flowers of five individuals the large/short pistil ratio was 15 : 1. Floral dimorphism is associated with pistil length, with a significant difference between the two morphs (t_{38} = 12.26; $P < 0.0005$). The short pistils are associated with reduction of the gynophore ($\bar{X}$ = 1.12, SD = 0.24 in large-pistil flowers and $\bar{X}$ = 0.54, SD = 0.09 in short-pistil flowers), of style

TABLE 2. Measurements of different floral characteristics of seven *Bauhinia* species (in cm). (1) Inferior and lateral petals; (2) upper or principal petals; (3) staminodes; (4) short style; (5) from Ramirez et al. (1984).

Section Species	N	Flower Length $\bar{X}$ (SD)	Flower Width $\bar{X}$ (SD)	Flower Color	Hypanthium $\bar{X}$ (SD)	Stamen length Long $\bar{X}$ (SD)	Stamen length Short $\bar{X}$ (SD)	Pistil length Gynophore $\bar{X}$ (SD)	Pistil length Ovary $\bar{X}$ (SD)	Pistil length Style $\bar{X}$ (SD)	Pistil length Stigma $\bar{X}$ (SD)
Pauletia (trees)											
B. aculeata	27	3.79 (0.30)	7.10 (0.39)	white (1, 2)	0.48 (0.11)	4.16 (0.25)	2.98 (0.22)	1.12 (0.24)	1.06 (0.09)	2.40 (0.20)	0.20 (0.00)
	13				0.42 (0.08)(4)	3.98 (0.31)	2.98 (0.19)	0.54 (0.09)	0.70 (0.10)	1.08 (0.18)	0.10 (0.00)
B. multinervia	5	10.53 (0.93)	9.78 (0.25)	white (1, 2)	3.04 (0.59)	7.28 (1.70)	6.10 (2.04)	4.50 (0.85)	2.34 (0.18)	3.92 (0.52)	0.78 (0.13)
B. pauletia	5	15.85 (1.14)	— —	white (1, 2)	1.20 (0.20)	7.20 (1.01)	2.87 (0.21)(3)	3.77 (0.76)	1.67 (0.15)	3.53 (0.29)	0.57 (0.15)
B. ungulata (5)	94	4.66 (0.65)	1.42 (0.22)	white (1, 2)	1.23 (0.17)	4.11 (0.39)	2.91 (0.45)	2.22 (0.46)	1.35 (0.32)	1.93 (0.65)	0.23 (0.07)
	20			red (3)	1.15 (0.14)(4)	4.12 (0.48)	2.80 (0.53)	1.60 (0.27)	1.12 (0.08)	1.12 (0.21)	0.18 (0.06)
Tylotaea (lianas)											
B. glabra	5	1.83 (0.45)	1.89 (0.42)	white (1) with purple lines (2)	— —	0.70 (0.00)	0.52 (0.05)	— —	0.34 (0.02)	0.29 (0.02)	0.05 (0.00)
B. guianensis	5	2.26 (0.03)	2.13 (0.02)	white (1) clear yellow (2)	— —	1.04 (0.05)	0.82 (0.08)	— —	0.43 (0.03)	0.36 (0.04)	0.05 (0.00)
B. rutilans	5	1.90 (0.20)	1.60 (0.28)	pink (1) yellow greenish (2)	— —	0.90 (0.07)	0.72 (0.08)	— —	0.43 (0.04)	0.30 (0.07)	0.05 (0.00)

($\bar{X}$ = 2.40, SD = 0.20; $\bar{X}$ = 1.08, SD = 0.18, respectively). The number of ovules per ovary is similar in both morphs but the ovules of short-pistil flowers are abortive. In *Bauhinia multinervia* there were no floral variations (Table 2).

The flowers of both sections are zygomorphic, the petals are different in form and size. In general, the inferior and lateral petals are similar in form, while their areas are slightly different (Table 3).

The flowers of sect. *Tylotaea* are smaller than those of sect. *Pauletia*; the average floral length varies from 1.83 to 2.26 cm. The gynophore and hypanthium are also shorter than in sect. *Pauletia*.

In *Bauhinia pauletia*, *B. multinervia*, and *B. ungulata*, one or two flowers open per night per inflorescence (Table 4). Anthesis, petal expansion, occurs at dusk between 1700 and 1900 hours, and the process is quick and synchronic (Fig. 1). *Bauhinia aculeata* has nocturnal anthesis but is comparatively asynchronous (2100–0300) and showed two peaks during anthesis (Fig. 1). In the species of sect. *Pauletia* anthers dehisce before anthesis.

In the species of sect. *Tylotaea* (lianas), anthesis is diurnal, occurring approximately between 0730 and 1130 hours. Petal expansion is slower, and the number of opened flowers per inflorescence per day is higher than in tree species of sect. *Pauletia* (Fig. 1). The pink flowers of *Bauhinia rutilans* showed two peaks during anthesis (Fig. 1). Although we did not record anthesis in *Bauhinia guianensis*, it occurs in the morning between 0900 and 1100 hours and is probably similar to that in *B. rutilans* (pers. obs.).

NECTAR SECRETION

In the arborescent *Bauhinia* species nectar is produced and accumulated in the hypanthium of flowers. Nectar production starts immediately after anthesis; however, in *B. multinervia* there was a little nectar before anthesis. The average volumes were high for *B. multinervia* (102.42 ml) and *P. pauletia* (47.32 ml); nectar concentration was relatively low and similar in the species studied (Table 5). The nectar of *B. aculeata* was produced during day and night; the average nocturnal production is significantly less than the diurnal production (t_6 = 8.55; $P < 0.0005$). This difference was associated with a diurnal floral activity higher than nocturnal. The solute concentration of nectar increased from the first hours after anthesis until midnight in *B. pauletia* and *B. multinervia*, while in *B. aculeata* the higher concentration of nectar occurred during the night period. The volume pro-

TABLE 3. Morphological characteristics of petals in six *Bauhinia* species. L = length, A = width.

Section Species	Inferior petals				Lateral petals				Upper petals			
	Area (cm²)	L (cm)	A (cm)	L/A ratio	Area (cm²)	L (cm)	A (cm)	L/A ratio	Area (cm²)	L (cm)	A (cm)	L/A ratio
Pauletia (trees)												
B. aculeata	8.23	6.15	2.15	3:1	7.19	5.80	2.12	3:1	1.95	1.95	1.95	3:1
B. multinervia	11.43	10.55	1.60	6:1	7.92	8.90	1.45	6:1	1.40	1.40	1.40	6:1
B. pauletia	0.61	9.20	0.08	6:1	0.37	3.10	0.08	6:1	0.18	0.18	0.18	6:1
Tylotaea (lianas)												
B. glabra	0.80	1.67	0.90	2:1	0.58	1.65	0.75	2:1	0.50	0.50	0.50	3:1
B. guianensis	1.74	2.00	1.30	1.5:1	0.58	1.80	1.25	1.2:1	0.40	0.40	0.40	6:1
B. rutilans	0.87	2.00	0.70	3:1	0.66	1.90	0.65	3:1	0.60	0.60	0.60	3:1

Section Species	Inferior petals				Lateral petals				Upper petals			
	Form				Form				Form			
Pauletia (trees)												
B. aculeata	narrowly elliptic				narrowly elliptic				lanceolate			
B. multinervia	lanceolate				lanceolate				very narrowly elliptic			
B. pauletia	narrowly oblanceolate				narrowly oblanceolate				narrowly oblanceolate			
Tylotaea (lianas)												
B. glabra	narrowly obovate				narrowly obovate				oblanceolate			
B. guianensis	very elliptic				suborbiculate				very narrowly elliptic			
B. rutilans	narrowly elliptic				narrowly elliptic				oblanceolate			

TABLE 4. Floral biology and visiting agents of six species of *Bauhinia*. (1) = bats, (2) = birds, (3) = insects, (4) = with pollen load, (5) = not identified.

Section Species	Observation hours	Anthesis hours	Number of opened flowers/inflorescences/day			Time of floral receptivity	Flower longevity	Visiting agents
			Range	$\bar{X}$	SD			
Pauletia								
B. aculeata	30	2100–0300	1–2	1.15	0.36	Nocturnal and diurnal	16 hr.	Apodiformes (2) Trochilidae *Chrysolampis mosquitus* Coleoptera (3) Scarabidae *Leucothyreus* sp. (4) Hymenoptera (3) Anthophoridae *Xylocopa* (*Neoxylocopa*) sp. (4) *Xylocopa fimbriata* Fab. Apidae *Apis mellifera* L. (4) *Eulaema speciosa* (Mocsary) (4) Lepidoptera (3) Hesperiidae *Epargyreus* sp. (4) Noctuidae (5) Pieridae *Anteos clorindae* Godart. (4) *Aphrissa statica* Cramer *Eurema nise* Cramer *Ganyra menciae* var. *janeta* (Dixey) (4) Sphingidae *Eumorpha labruscae* (L.) (4) *Eumorpha vitis* (L.) (4)
B. multinervia	29	1700–1830	1	1.00	0.00	Nocturnal	18 hr.	Chyroptera (1) Phyllostomatidae *Phyllostomus discolor* Wagner (4) *Glossophaga soricina* Pallas (4)

TABLE 4. Continued.

Section Species	Observation hours	Anthesis hours	Number of opened flowers/inflorescences/day Range	$\bar{X}$	SD	Time of floral receptivity	Flower longevity	Visiting agents
								Apodiformes (2) Trochilidae *Phaethornis agusti* Hymenoptera (3) Apidae *Apis mellifera* L. (4) *Apis mellifera* var. *scutellata* Lat. (4) Vespidae *Synoeca surinama* L. Lepidoptera (3) Hesperiidae
B. pauletia	17	1730–1900	1–2	1.05	0.21	Nocturnal	13 hr.	Chyroptera (1) Phyllostomatidae *Phyllostomus discolor* Wagner (4) *Glossophaga soricina* Pallas (4) Hymenoptera (3)
Tylotaea								
B. glabra	32	0530–0900	1–7	2.51	1.63	Diurnal	24 hr.	Hymenoptera (3) Anthophoridae *Xylocopa* (*Neoxylocopa*) sp. (4) Apidae *Apis mellifera* L. (4) *Centris* (C.) *aenea* Lepeletier (4) *Trigona* nr. *cupira* Smith (4) Formicidae *Pseudomirmex* sp. grupo *gracilis* Halictidae *Pseudaugochloropsis* sp. (4) Vespidae *Polybia ignobilis* (Holiday) (4) Lepidoptera (3) Hesperiidae

TABLE 4. Continued.

Section Species	Observation hours	Anthesis hours	Number of opened flowers/inflorescences/day			Time of floral receptivity	Flower longevity	Visiting agents
			Range	$\bar{X}$	SD			
B. guianensis	12	0900–1100	—	—	—	Diurnal	9 hr.	Apodiformes (2) Trochilidae ? Hymenoptera (3) Apidae *Trigona williana* Friese (4) Anthophoridae *Gaesochira complanata* Moure & Michener (4) Halictidae *Megalopta* sp. (4) Vespidae *Polybia occidentalis* (4) *Synoeca surinama* L. (4) *Steiopolybia pallipes* Olivier Lepidoptera (3) Hesperiidae *Nastra insignis* (Ploetz)
B. rutilans	16	0430–1100	—	—	—	Diurnal	24 hr.	Apodiformes (2) Trochilidae *Schistes geoffroyi* L. Hymenoptera (3) Anthophoridae *Xylocopa* sp. (4) Apidae *Bombus* sp. (4) *Trigona fulviventris* Guerin Eumeninae (5) Vespidae *Stenodynerus* sp.

duced can exceed the volume of the hypanthium cavity, and without pollinating visits, nectar starts dripping down or out. *Bauhinia aculeata* produced nectar for 19 hours, whereas in *B. pauletia* and *B. multinervia*, production lasted approximately 13 hours. The secretion rate, estimated as the volume produced per time unit, was highest in *B. multinervia* ($\bar{X}$ = 7.88 ml/hr.), followed by *B. pauletia* ($\bar{X}$ = 3.61 ml/hr.) and *B. aculeata* ($\bar{X}$ = 0.27 ml/hr.). The first two species are characterized by nocturnal secretion. Significantly in *B. aculeata* no difference between diurnal (0.17 ml/hr.) and nocturnal (0.22 ml/hr.) secretion rates was found.

The species of sect. *Tylotaea* produced less volume of nectar with a higher sugar concentration than those of sect. *Pauletia* (Table 5). In *Bauhinia glabra* the volume was less than the minimal capacity of microcapillaries and only a sticky sap at the base of stamens and pistil was detected. In *B. rutilans* nectar secretion took place during seven hours and the rate was 0.27 ml/hr., similar to that in *B. aculeata* (sect. *Pauletia*), with a total of 1.88 ml per flower.

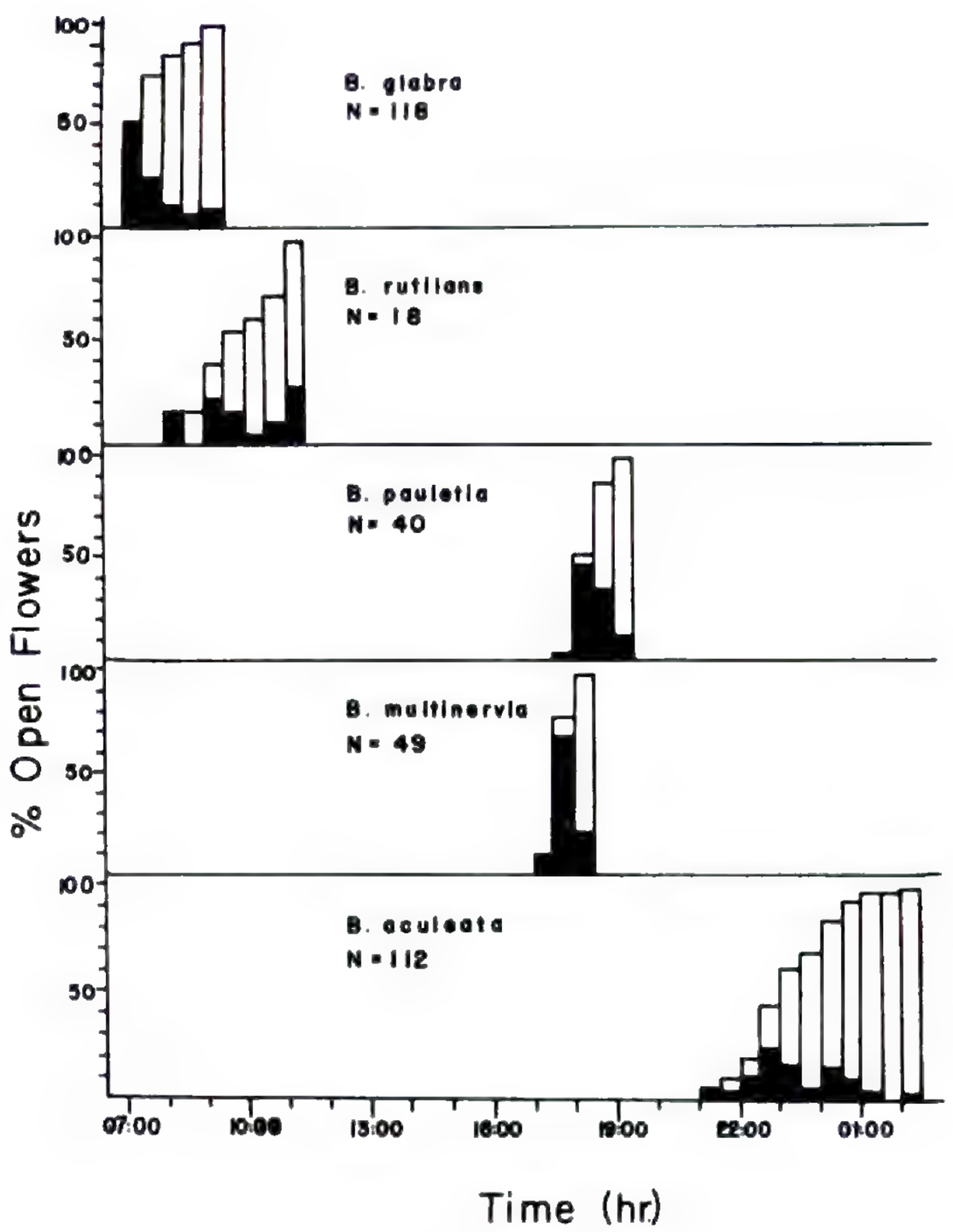

FIGURE 1. Anthesis expressed as the percentage of open flowers during half-hour intervals. □ % cumulative, ■ % non-cumulative.

NECTAR COMPOSITION

The nectar of six *Bauhinia* species contained proteins, amino acids, phenols, and alkaloids, but no lipids were detected in the nectar of any of the species studied (Table 6). Alkaloids appeared in low quantities only in the nectars of *B. aculeata* and *B. rutilans*.

Only traces of protein were detected in the nectar of *B. multinervia* (sect. *Pauletia*), while in *B. glabra* and *B. rutilans* (sect. *Tylotaea*) it was detected in low quantities. The proportion of sugar in the nectar of sect. *Pauletia* showed that sucrose is dominant in *B. aculeata*, while *B. multinervia* and *B. ungulata* were hexose-dominant with similar proportions of glucose and fructose. The proportion of glucose was similar to sucrose in *B. glabra* but there was a higher proportion of both sugars than of fructose (Table 7).

There is a temporal change of the proportion of sucrose, glucose, and fructose in the nectars during the secretion period, with a decrease in the proportion of sucrose over time in the tree species. At the beginning of nectar secretion, the proportion of sucrose was 2.74 times higher than 12 hours later in *B. pauletia*, *B. multinervia* (both sect. *Pauletia*), and *B. rutilans* (sect. *Tylotaea*): when sucrose decreases, fructose and glucose increase in quantity and the sucrose/glucose + fructose ratio decreases (Table 7).

The proportions of 20 amino acids analyzed differed in the nectar of different *Bauhinia* species, and varied from 3 to ≥ 10, using a relative scale (Table 6). The scale from 1 to 10 is based on standard concentrations of histidine. A value of 10 is equivalent to 3.9 mg histidine/ml, and each successive unit below 10 represents a halving of concentration (9 = 1.95 mg/ml; 8 = 0.975 mg/ml; and so forth) (Baker & Baker, 1975). The analyses showed that there was no difference in the presence of essential amino acids. Proline was dominant in all species except *B. multinervia*. Only one species studied, *B. rutilans*, had lysine in the nectar (Table 8).

POLLINATOR ACTIVITY

In bat-pollinated species of *Bauhinia* the flowers are exposed on the top of the foliage, and petals are separated, leaving the anthers exposed. The pollen adheres to the head and ventral part of the animal. The feeding activity and hence pollination last only seconds with the maximum occurring at dusk and in the first night hours. During the visit, *Phyllostomus discolor* and *Glossophaga soricina* seize the flowers and inflorescences so that the branches are bent down by the weight of the animal. Nocturnal visits were made by Sphingidae and but-

TABLE 5. Average volume and solute concentration of nectar for five *Bauhinia* species.

Section / Species	Total volume of nectar (ml/flower)			Solute concentration (%)		
	Range	$\bar{X}$	SD	Range	$\bar{X}$	SD
Pauletia (trees)						
B. aculeata	3.96–5.81	5.03	0.95	12.0–28.0	19.35	4.85
B. multinervia	60.37–138.01	102.42	36.41	16.4–21.0	19.34	1.62
B. pauletia	14.18–87.44	47.32	37.12	13.0–18.0	16.23	2.07
Tylotaea (lianas)						
B. glabra	—	<0.24	—	—	≥30.00	—
B. rutilans	1.06–2.36	1.88	0.57	26.0–30.0	28.25	1.81

terflies, and phyllostomatid bats were observed on *B. multinervia* and *B. pauletia* flowers. *Phyllostomus discolor* and *Glossophaga soricina* bats were considered effective pollinators because they carried pollen on their heads and bodies (Table 4). During the day, the flowers of *B. multinervia* and *B. pauletia* were visited by butterflies, wasps, and hummingbirds, though there was little nectar and pollen. In addition, *B. multinervia* was visited between 0530 and 0800 hours by *Phaethornis aguti* (Trochilidae) to take nectar of open flowers from the previous night.

A different behavior was shown for *Bauhinia aculeata* (sect. *Pauletia*): during the night, flowers were visited by Sphingidae (*Eumorpha labruscae* and *E. vitis*) and infrequently by Noctuidae. Butterflies, wasps, bees, and hummingbirds were abundant during the day. The bees, *Xylocopa* (*Neoxylocopa*) sp., *Apis mellifera*, *Eulaema speciosa*, and several species of Pieridae (e.g., *Anteos clorindae*, *Ganyra menciae*) carried pollen of *B. aculeata*. These insects inserted their heads inside the flower and imbibed nectar. The hummingbird *Chrysolampis mosquitus* took nectar from the flower in the morning between 0600 and 0730 hours and at dusk between 1600 and 1830 hours.

The species of sect. *Tylotaea* have comparatively small flowers, which were visited by a great variety of bees, wasps, butterflies, and hummingbirds during the time of stigma receptivity (Table 4). *Bauhinia glabra* was visited by *Apis mellifera* and *Pseudaugochloropsis* sp. These insects arrived at the flowers posing on the inferior and lateral petals, introducing their body into the flower, while *Bombus* sp. inserts only its head into the flower. The most frequent visits were by *A. mellifera* and *Bombus* sp. during the morning.

Bauhinia guianensis was visited by *Xylocopa* sp. and *Synoeca surinama* in the morning and afternoon. These bees carried pollen on the legs and head. A species of butterflies (*Nastra insignis*, Hesperiidae) took nectar about noon, but it was not a pollinator. In addition, one unidentified hummingbird was observed for a long time visiting the flowers. *Bauhinia rutilans* was visited by bees, wasps, and hummingbirds; *Xylocopa* sp. and *Bom-*

TABLE 6. Proportion of organic compounds in nectar of six *Bauhinia* species (arrows indicate temporary trends after anthesis).

Section / Species	Amino acids[1]	Phenols	Alkaloids	Proteins
Pauletia (trees)				
B. aculeata	6	tr	slightly+	ND
B. multinervia	5 → ≥10*	± → ++	ND	tr
B. pauletia	3 → 7	tr → +	ND	ND
B. ungulata	6	tr	ND	ND
Tylotaea (lianas)				
B. glabra	6 → >10	+	ND	tr
B. rutilans	3 → 7	+ → ++	slightly+	+

tr = traces; * = suggests breakdown during the night; ND = not detected; [1] = scale from 1 to 10 of relative quantities; + = moderate; ++ = abundant.

TABLE 7. Proportion of nectar sugars and their temporal variation (variations in time are in the direction of the arrows after anthesis).

Section Species	Proportion of sugars					Sucrose/ glucose + fructose
	Melezitose	Maltose	Sucrose	Glucose	Fructose	
Pauletia (trees)						
B. aculeata	—	—	0.552	0.241	0.208	1.279[a]
B. multinervia	0.005 → 0.111	—	0.167 ← 0.211	0.329 → 0.446	0.368 → 0.460	0.203 ← 0.413[b]
B. pauletia	—	—	0.188 ← 0.516	0.279 → 0.463	0.206 → 0.349	0.246 ← 0.153[b]
B. ungulata	0.016	0.006	0.185	0.443	0.350	0.233[b]
Tylotaea (lianas)						
B. glabra	0.007	—	0.330	0.388	0.274	0.499[c]
B. rutilans	—	—	0.365 ← 0.558	0.234 → 0.369	0.208 → 0.224	0.573 ← 1.261[a]

[a] sucrose dominant, [b] hexose dominant, [c] intermediate between a and b.

bus sp. were abundant collecting pollen during the middle of the day. The flowers were visited frequently by *Schistis geoffroyi* (Trochilidae) and the pollen was collected on their bills. In addition, the flowers were perforated externally at the base by an unidentified nectar-robbing species of hummingbird.

DISCUSSION

The morphology, color, and scent of flowers are associated with size and behavior of pollinators. Chiropterophilous flowers are often white, exposed above the foliage, nectar continuously, show nocturnal anthesis, and have a disagreeable smell (e.g., Heithaus et al., 1974; Sazima & Sazima, 1975, 1978; Voss et al., 1980; Howell & Schropfer Roth, 1981; Ramirez et al., 1984). Entomophilous species, including those of *Bauhinia*, have flowers of smaller size, of varied color, fragance, diurnal anthesis, and low nectar production. In addition, bee flowers often have dense inflorescences (e.g., Bolten & Feinsinger, 1978; Frankie et al., 1983). Such floral characteristics as flower size and time of anthesis of the studied *Bauhinia* species can be related to their different pollination systems. The white-flowered *Bauhinia pauletia* and *B. multinervia* are chiropterophilous, and *B. glabra* and *B. guianensis* are entomophilous, while the pink flowers with red bracts of *B. rutilans* were visited frequently by hummingbirds, which carry pollen.

In most chiropterophilous species, anthesis seems to occur at dusk (1800–2000 hours) (Heithaus et al., 1974; Sazima & Sazima, 1975; Gould, 1978; Lack, 1978; Ramirez et al., 1984). Anthesis of *Bauhinia pauletia* and *B. multinervia* occurred at similar evening hours. The flowers last one night, similar to *Markea neurantha* (Solanaceae) (Voss et al., 1980), *Lafoensia pacari* (Lythraceae) (Sazima & Sazima, 1975), and *Bauhinia ungulata* (Ramirez et al., 1984). In *Passiflora mucronata* (Passifloraceae) anthesis occurs between 0100 and 0200 hours, with a duration of less than 12 hours (Sazima & Sazima, 1978). The nocturnal flowers of *Bauhinia* can be considered as synchronic in anthesis because more than 50% of the flowers open within 30 minutes. The total process occurs in two and one-half hours. Anthesis of *Bauhinia glabra* and *B. rutilans* is diurnal, unimodal, and asynchronous, the peak of flower opening involving less than 40% of the flowers.

In *Bauhinia aculeata*, anthesis is nocturnal and asynchronous, with two peaks of less than 40% each; this asynchronic anthesis could promote cross-fertilization; the flowers are visited by a variety of pollinators. *Bauhinia aculeata* showed a combination of floral features: the floral morphology, nectar chemistry, timing of anthesis, and the pattern of nectar production cannot be placed with the other species studied. *Bauhinia aculeata* could be intermediate between nocturnal and diurnal pollination because a great number of specialized and unspecialized diurnal and nocturnal floral visitors and pollinators are associated with this species.

In bat-pollinated plants, higher production of nectar has been reported than in hummingbird- and butterfly-pollinated plants, and nectar production is continuous (Cruden, 1976; Baker, 1978). Nectar production in *Bauhinia pauletia* and *B. multinervia* is higher than in *Ochroma*, *Parkia*, *Chiranthodendron*, and *Lafoensia pacari*, which produce 5 to 20 ml/flower or inflorescence (Heithaus et al., 1975; Sazima & Sazima, 1975; Voss et al., 1980).

Flowers visited by bees frequently produce low nectar quantities. Frankie et al. (1983) found dif-

TABLE 8. Amino acid composition in nectar of six species of *Bauhinia*.

Section Species	Amino acids												
	Ala*	Argo	Asp	Aspt	Cys	Glu	Glut	Gly*	Histo	Isolo	Leuo	Lyso	Meto
Pauletia (trees)													
B. aculeata	+	+	+	?	+	+	+	+	±	+	+	ND	+
B. multinervia	+	±	+	?	+	+	+	+	±	+	±	ND	+
B. pauletia	+	+	++	+	+	+	+	+	?	+	+	ND	+
B. ungulata	+	±	+	ND	+	+	+	+	ND	ND	ND	ND	+
Tylotaea (lianas)													
B. glabra	±	+	+	+	+	+	+	+	ND	?	?	ND	+
B. rutilans	+	+	tr	ND	ND	+	ND	+	ND	tr	tr	+	?

o = essential amino acids for insect nutrition
* = amino acids in nectar of hummingbird-pollinated plants
tr = traces
ND = not detected
++ = strong
+ = good
± = moderate

ferent flower sizes associated with the daily nectar production. These authors defined moderate nectar production as 1.0 to 8.0 μl/day and high nectar production as on average higher than 8.0 μl/day. In addition, bee plants with elevated concentrations of solutes have small flowers and low nectar production (Hainsworth & Wolf, 1972; Baker, 1975). However, *Bauhinia glabra* and *B. rutilans* differ from this expectation since they produce higher volumes of nectar than those reported by Frankie et al. (1983). In addition, the visits and pollen load on *Schistis geoffroyi* (Trochilidae) suggest the importance of birds in the pollination systems of *B. rutilans* at the canopy level, so this species cannot be considered as a strictly melitophilous species.

The solute concentration of bat-pollinated flowers is frequently low (Howell, 1975, 1978; Baker, 1978; Steiner, 1983), and an increase of solutes from early to later hours after anthesis has been reported, e.g., in *Lafoensia pacari* from 6.8% to 11.0% (Sazima & Sazima, 1975). By contrast, Ramirez et al. (1984) showed in *Bauhinia ungulata* a higher solute concentration immediately before anthesis, which then decreased from 15.4% to 12.0%.

Percival (1965) found an increase in solute concentration with flower age in species of sect. *Tylotaea* and *B. aculeata* (sect. *Pauletia*). The increase in nectar concentration can increase the exploitation efficiency in flowers with low quantities of nectar (Hainsworth & Wolf, 1976). The nectar concentration of *Bauhinia multinervia* and *B. pauletia* flowers decreased with flower age. In the chiropterophilous species the visits are probably more frequent at the first hours after anthesis. In contrast, nectar concentrations of melitophilous-ornithophilous species (*B. glabra* and *B. rutilans*, respectively) increased at the midday hours. The increase of nectar concentrations and the higher pollination activities could be related to the temperature elevation during midday hours and concomitant evaporation from the nectar. Bees and hummingbirds prefer nectar up to 20% or 40% of sugar concentration (Percival, 1974; Baker, 1975).

The flowers of sect. *Pauletia* produce nectar during approximately 12 hours. Heithaus et al. (1974) reported a rate of nectar secretion of 0.5 ml/hr. for the first hours of production (from 1800 to 2300) in *B. pauletia*; however, the total rate of nectar secretion was 3.16 ml/hr. *Bauhinia pauletia* and *B. multinervia* showed a higher rate than *B. ungulata* (Ramirez et al., 1984). The difference could be associated with the greater flower and hypanthium cavity sizes of the first two species.

Nectar has a variety of nutritional compounds (Percival, 1965) and elements with a selective function (Baker & Baker, 1975). The alkaloids in *Bauhinia aculeata* (sect. *Pauletia*) and *B. rutilans* (sect. *Tylotaea*) probably reflect a selective force at pollination level. The high diversity of visiting agent species in both plant species could be selected by deterrent compounds. The absence of nectar proteins in the species of sect. *Pauletia* is related to bat pollination because some pollinating bat species eat insects (Heithaus et al., 1975) and pollen as a protein source (Alvarez & Quintero, 1969; Howell, 1974). In contrast, the nectars of

TABLE 8. Continued.

Amino acids						
Pheo	Pro*	Ser*	Tyr	Treoo	Tripo	Valo
+	++	+	+	+	±	+
+	+	+	?	+	+	+
±	±	+	±	+	+	+
+	++	+	ND	+	ND	±
+	++	+	+	+	?	+
ND	tr	tr	ND	tr	+	+

the species of sect. *Tylotaea* have some proteins; the insects that visit these species presumably obtain their nitrogenous requirement mainly from nectar and pollen, while hummingbirds obtain their nitrogenous requirement from nectar.

Flowers pollinated by butterflies and hummingbirds are reported as rich in sucrose, while nectar of bat flowers tends to be rich in hexose (Baker, 1978), and the nectar of bee flowers has no definite pattern in sugar proportions. *Bauhinia multinervia*, *B. pauletia*, and *B. ungulata* are hexose-dominant chiropterophilous species and have nocturnal nectar secretion. In these species, sucrose decreases with time, and glucose and fructose increase simultaneously. This pattern suggests a breakdown of sucrose, and then the sucrose/glucose + fructose ratios decrease. The breakdown of sucrose can be considered an advantage for pollination because bats cannot assimilate sucrose (Harborne, 1977). This pattern has been found in *B. rutilans* but was associated with hummingbird and bee pollination. *Bauhinia glabra* is rich in sucrose and glucose and has an entomophilous pollination system.

The flower morphology, floral biology, pollinator species, nectar composition, and timing and amount of secretion are associated with life form and subgeneric designation of the *Bauhinia* species studied. The species of sect. *Pauletia* are trees or shrubs, frequently pollinated by bats. In contrast, the species of sect. *Tylotaea* are lianas, pollinated by insects and birds. The pollinator specificity among *Bauhinia* species with similar pollinators is achieved basically through their geographic distributions. Sympatric distribution and overlapping flowering periods were found only for *Bauhinia* species of different sections. In this sense, the most important attribute is floral morphology. The floral characteristics and pollination biology provide additional characters for *Bauhinia* systematics. The agreement among reproductive and taxonomic properties could be related to evolutionary patterns at the sectional level.

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ADICIONES A LAS PAPILIONADAS DE LA FLORA DE NICARAGUA Y UNA NUEVA COMBINACION PARA OAXACA, MEXICO[1]

Mario Sousa S.[2]

Resumen

Se describen dos especies nuevas para la ciencia. Se hace dos nuevas combinaciónes y se tipifican dos especies en la familia Leguminosae para la *Flora de Nicaragua*; también se produce una nueva combinación para la de Oaxaca, México. Estas corresponden a las Papilionoideae, de estas nuevas especies una pertenece a la tribu de las Sophoreae (*Styphnolobium caudatum*) y otra a la de las Millettieae (*Lonchocarpus bicolor*). Las nuevas combinaciones son una en las Sophoreae (*Styphnolobium conzattii*) y otra en Aeschynomeneae (*Diphysa americana*). Se tipifican a dos Millettieae: *Lonchocarpus macrocarpus* Benth. y *L. parviflorus* Benth.

Abstract

Two new species are described, two new combinations are made, and two species are typified within the family for the *Flora de Nicaragua*. Also a new combination is made for the *Flora de Oaxaca, Mexico*. These belong to the Papilionoideae, of which *Styphnolobium caudatum* belongs to the tribe Sophoreae, and *Lonchocarpus bicolor* belongs to the tribe Millettieae. Of the two combinations, *Styphnolobium conzattii* belongs to the Sophoreae, and *Diphysa americana* to the Aeschynomeneae. Two species belonging to the Millettieae are typified: *Lonchocarpus macrocarpus* Benth. and *L. parviflorus* Benth.

A partir de la publicación "Adiciones a las leguminosas de la *Flora de Nicaragua*" (Sousa, 1986 [1987]) se han hecho nuevas colectas que añaden dos especies más al grupo de géneros de leguminosas que se nos invitó a participar en el proyecto *Flora de Nicaragua*, también ha sido necesario hacer nuevas combinaciones y tipificar taxa descritos con elementos heterogéneos. A pesar de tratarse de adiciones a la *Flora de Nicaragua*, se hace una nueva combinación de una especie endémica de Oaxaca, México; se tomó esta libertad, dado que de otra forma no se comprende adecuadamente el concepto y la circunscripción del género *Styphnolobium* para México y Mesoamérica. Es también de notarse que a *Diphysa* se le ubica en la tribu de las Aeschynomeneae en vez de las Robinieae; ésto es debido a los recientes estudios que viene realizando Matt Lavin (1987) y que parecen justificar este cambio.

Sophoreae

Styphnolobium caudatum M. Sousa & Rudd, sp. nov. TIPO: Nicaragua. Estelí: Salto de Estanzuela, 6 km al S de Estelí, 13°02′N, 86°22′O, 29 mayo 1985, *M. Sousa 12985, G. Davidse, P. P. Moreno & A. Grijalva* (holotipo, MEXU; isotipos, BM, HNMN, MO). Figura 1.

Arbores altae; cortex squamosus placoideus irregularis, cinereus. Folia 9–13-foliolata; foliola stipellis minutis oblongis, chartacea, lanceolata, 4–9 cm longa, (1.3–)2–2.7 cm lata, apice longiacuminato vel caudato, margine applanato. Infructescentiae pendentes, axillares, 12–17 cm longae. Legumen stipitatum, torulosum, homogeneum, 5–14 cm longum, 2.3–2.7 cm diametro, dense ferrugineo-velutinum, 1, 2(–4)-seminale.

Árbol de más de 30 m de alto; corteza escamosa placoide irregular, con tonos metálicos, con abun-

[1] Se agradece por aceptar colaborar con el autor a la Dra. V. E. Rudd; por facilitar todo lo necesario para llevar a cabo este trabajo, al Dr. W. D. Stevens, editor y ejecutor del proyecto *Flora de Nicaragua*; al Dr. F. Chiang por traducir las diagnosis al latín; al Sr. Daniel Cobian C., quien logró una muy buena lámina; a Mario Sousa Peña por incorporar el manuscrito a un procesador de textos; al Dr. A. O. Chater por proporcionar copia de la lámina de Plukenet; y a los curadores de BM, BR, F, G, K, MEXU, MICH, MO, y US por facilitar el material botánico para su estudio.

[2] Herbario Nacional, Instituto de Biología, U.N.A.M., Apartado Postal 70-367, Coyoacán, 04510, México D.F. México.

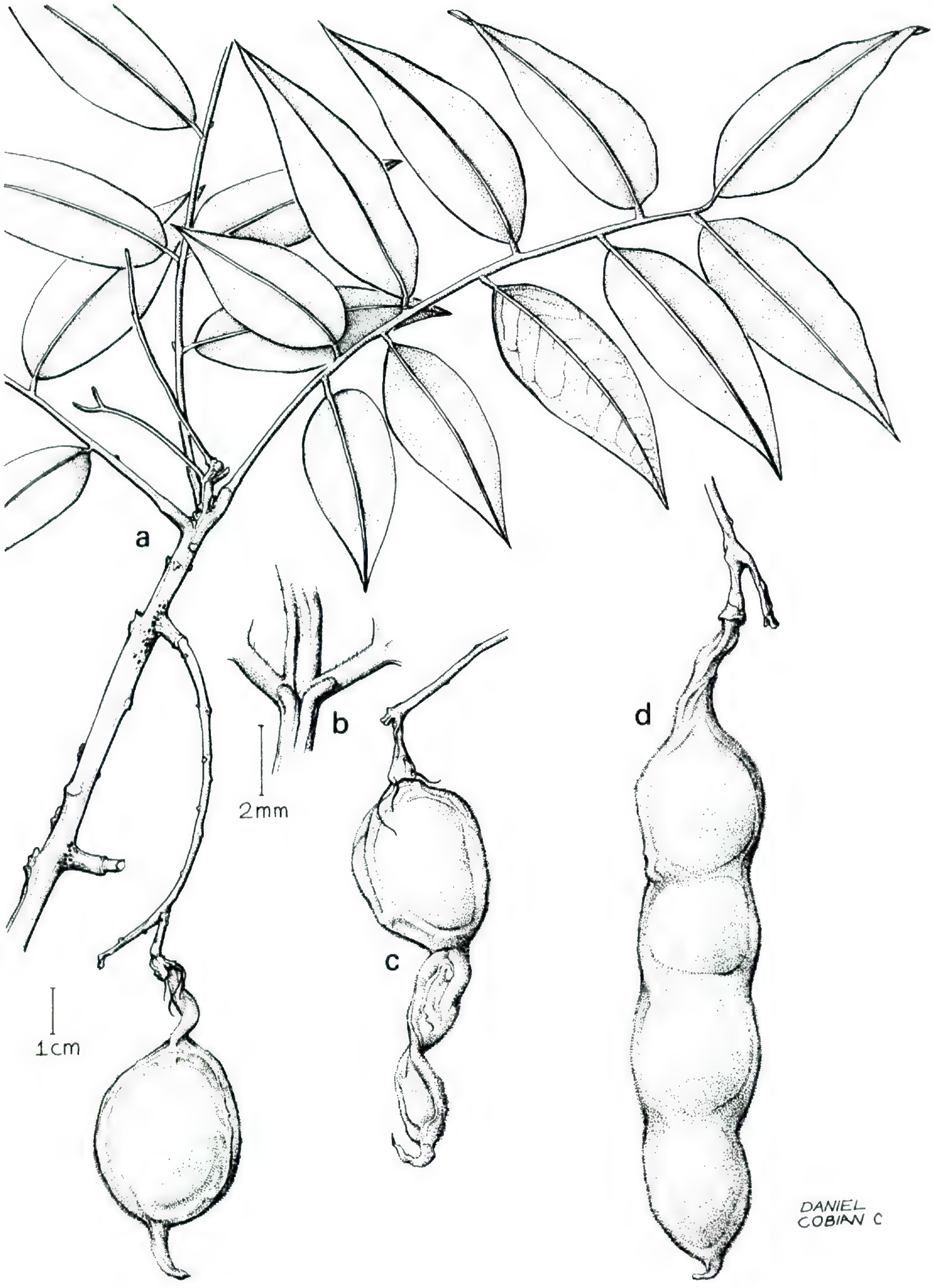

FIGURA 1. *Styphnolobium caudatum*.—a. Rama con infrutescencia.—b. Detalle de estipelas y pulvínulos.—c. Legumbre monosperma.—d. Legumbre tetrasperma. Tomado de *Sousa 12985*.

dantes lenticelas prominentes; ramas jóvenes minutamente velutinas pronto esparcidamente, gris claro; lenticelas orbiculares, cremas. Hojas 9–13-folioladas; estípulas caducas, no vistas; pecíolo 2.5–5.5 cm de largo; raquis 7–15 cm de largo; folíolos estipelados, estipelas hasta 8 mm de largo, oblongas, pronto caducas; láminas cartáceas, lanceoladas, 4–9 cm de largo, (1.3–)2–2.7 cm de ancho, base redondeada ligeramente asimétrica, en ocasiones cuneada, ápice largamente acuminado a caudado, márgenes planos, glabros en al haz y esparcidamente seríceos en el envés, nervaduras secundarias 10–13, inconspicuas. Infrutescencias axilares, péndulas, racemosas, simples o ramificadas, 12–17 cm de largo, pedicelos 5–9 mm de largo. Legumbre torulosa, homogénea, estipitada, 5–14 cm de largo, 2.3–2.7 cm de diámetro, densamente ferrugíneo velutina, estípite hasta de 4 cm de largo; 1, 2(–4) semillas por fruto (semillas maduras no fueron vistas).

Distribución. Sólo de la localidad tipo en Estelí, de un sólo árbol, en una cañada húmeda, en la vega de un río, a 900 m de altitud. Con frutos inmaduros durante mayo.

Muestras adicionales examinadas. NICARAGUA. ESTELÍ: Salto de Estanzuela, 6 km al S de Estelí, 13°02′N, 86°22′O, 11 mayo 1985, *P. P. Moreno 25655* (MEXU, MO).

Styphnolobium conzattii (Standley) M. Sousa & Rudd, comb. nov. *Sophora conzattii* Standley, Contr. U.S. Natl. Herb. 23: 436. 1922. *Calia conzattii* (Standley) Yakovl., Proc. Leningr. Chem.-Pharm. Inst. 21: 45. 1967. TIPO: México. Oaxaca: *C. Conzatti 3171* (holotipo, US; isotipo, herbario Conzatti).[3]

Especie hasta ahora conocida del Cerro Espino en la Sierra Madre del Sur, muy característica por tener las flores de gran tamaño. Hasta hace poco fue colectada en fruto, lo que permitió su ubicación taxonómica en *Styphnolobium*. A esta especie Rudd (1971) le asignó en *Sophora* una sección propia, *Oresbios*, distinguiéndola por sus caracteres vegetativos y florales, desconociéndose en ese momento su fruto.

Por otro lado, Yakovlev (1967, 1968) revivió al género *Calia* de Terán & Berl., incluyendo en él a cinco especies americanas de *Sophora*, comprendiendo a *C. conzattii*, de la cual comenta: "parece sólo existir un ejemplar, el cual nosotros no contamos, es posible que esta especie sea una subespecie de *S. secundiflora*, pero hay que estudiar mejor este asunto."

Calia es separada de *Sophora* y géneros afines por contar con un cáliz bilabiado y fruto seco, caracteres ausentes en *C. conzattii* y mucho menos puede considerarse coespecífica de *S. secundiflora*.

Muestras adicionales examinadas. MÉXICO. OAXACA: Cerro Espino, Finca Montecristo, 23 abril 1976 (fr), *M. Sousa 5598* (MEXU); 5 abril 1984 (fr), *R. Torres C. 4901* (MEXU); 31 mayo 1984 (fl), *Torres 5231* (MEXU).

MILLETTIEAE

Lonchocarpus bicolor M. Sousa, sp. nov. TIPO: Nicaragua. Zelaya: near Lago Siempre Viva, 12 km SW of Bonanza, 14 May 1978, *D. Neill 4038* (holotipo, MEXU; isotipo, MO).

Arbores foliis deciduis; cortex interior ubi incisus succum resinaceum emittens; rami juniores dense ferrugineo-velutini. Folia 7-foliolata stipulis deciduis orbiculatis vel ligulatis 2.5–3 mm longis; petiolus elongatus; foliola epunctata, elliptico-oblonga, 11–15 cm longa, 5–6 cm lata, apice acuminato, valde bicoloria. Inflorescentiae pedunculatae, florescentia praecoci; pedunculi florales ad 2 mm longi; pedicelli ad 2.5 mm longi, bracteolis subopositis vel alternis a calyce remotis, filiformibus, parvis. Flores 9.5–11 mm longi; calyx epunctatus, paene truncatus, tribus dentibus carinalibus tantum; corolla epunctata, vexillo erecto et concavo; antherae glabrae; ovarium sericeum 4-ovulatum. Legumen (immaturum) ut videtur indehiscens, coriaceum, ellipticum vel oblongum, base attenuata, apice rotundato et rostrato, 1–2-seminale, luteo-velutinum, sutura vexillari anguste alata, ala ad 1.5 mm lata.

Arboles de 20 m de alto; caducifolios; la corteza interior con fluido resinoso al corte; ramas jóvenes acostilladas, densamente ferrugíneo velutinas, lenticelas poco visibles por la densa pelosidad, posteriormente glabrescentes. Hojas estipuladas, estípulas pronto caducas, erectas, orbiculares a liguladas, 2.5–3 mm de largo; pecíolo 4.5–8.5 cm de largo; raquis foliar velutino como las ramas jóvenes, 7–11 cm de largo; hojas 7-folioladas; folíolos cartáceos, epunteados, elíptico-oblongos, 11–15 cm de largo, 5–6 cm de ancho, base ligeramente cuneada, ápice acuminado, marcadamente bicoloros, verdosos y glabrescentes en el haz y blanquecinos y densamente canescente seríceos en el envés, nervaduras laterales 9–11. Inflorescencias pedunculadas, 2.5–6 cm de largo, floración precoz; pedúnculos florales hasta 2 mm de largo; pedicelos hasta 2.5 mm de largo; bractéolas subopuestas a alternas, de la mitad al tercio superior del pedicelo, filiformes, 0.9–1.1 mm de largo. Flores 9.5–11

[3] Herbario privado de la familia Conzatti que aun se conserva en la Cd. de Oaxaca, México.

mm de largo; cáliz ciatiforme, epunteado, 3–3.5 mm de largo, 4.5–5 mm de ancho, moderadamente seríceo, casi trunco, sólo presentes los 3 dientes carinales, el medio 1 mm de largo; corola epunteada, todos los pétalos canescente seríceos; estandarte erecto, su lámina cóncava, orbicular, 8 mm de ancho, moderadamente pelosa en las venaciones de la superficie externa; anteras glabras; ovario seríceo, 4-ovulado. Legumbre (sólo se vió inmadura) aparentemente indehiscente, coriácea, de elíptica a oblonga, atenuada en la base, redondeada y rostrada en el ápice, lateralmente compresa; 1–2 semillas por fruto, 7–8 cm de largo, hasta 1.6 cm de ancho, amarillo velutina, sutura vexilar angostamente alada, ala hasta 1.5 mm de ancho, sutura carinal angostamente aquillada (semillas maduras no fueron vistas).

Distribución. Sólo conocida del Departamento de Zelaya en Nicaragua, en selvas húmedas, de altitudes entre los 40 a 300 m. Florece en marzo, e inicia la fructificación a partir de mediados de mayo.

Nombres vernáculo. Cerizo, palo de cera.

Muestras adicionales examinadas. NICARAGUA. ZELAYA: sur del Río Wawa, 60 km NO de Puerto Cabezas, 14°19′N, 83°56′O, *E. L. Little 25117* (MO); Francia Sirpi, 30 km SO de Waspán, 14°28′N, 84°03′O, *Little 25303* (MO).

Lonchocarpus macrocarpus Benth., J. Linn. Soc., Bot. 4 (Suppl.): 91. 1860. TIPO: "México" [Nicaragua]. *Herb. Pavón s.n.* [*J. Mociño*] (lectotipo, G, aquí redesignado).

Aquí se lectotipifica a *Lonchocarpus macrocarpus* Benth. con el ejemplar del *Herb. Pavón* (G), a pesar de que Pittier (1928) lo hizo con el de *A. Fendler 1861*, pero en forma mecánica, habiendolo escogido por ser el ejemplar de Venezuela, área que él estudiaba. Simplemente transcribió su diagnosis sin haber visto los sintipos de este binomio heterogéneo, del cual, el de *Fendler* corresponde a *L. hedyosmus* Miq. s. lat., binomio más antiguo que el de *L. macrocarpus* Benth., el cual, pasaría como sinónimo. Por otro lado, el escoger al del *Herb. Pavón* se evita crear otro nuevo nombre y se estaría en mayor concordancia con el sentido que Bentham le dió al epíteto, dado que el material del Herb. Pavón en efecto cuenta con el fruto de mayor tamaño que el resto del material que Bentham vió. Esta especie ha sido confundida con *L. costaricensis* Pittier.

Lonchocarpus parviflorus Benth., J. Linn. Soc., Bot. 4 (Suppl.): 89. 1860. TIPO: [Nicaragua]. Segovia: *A. S. Oersted 2* (lectotipo, K, aquí designado).

Lonchocarpus orotinus Pittier, Contr. U.S. Natl. Herb. 20: 74, 75, pl. 5A, fig. 25. 1917. TIPO: Costa Rica. Guanacaste: Salinas Bay, *A. Tonduz 2731* (holotipo, US; isotipos, BM, BR).

Lonchocarpus whitei Lundell, Wrightia 1(2): 154, 155. 1946. TIPO: Nicaragua. Chinandega: along Río Acome, *S. S. White & C. L. Gilly 5385* (holotipo, MICH).

Lonchocarpus parviflorus fue descrito por Bentham en base a elementos heterogéneos sin definir al holotipo, así tenemos que el sintipo de *C. Jurgensen 219* (K) corresponde a *L. lanceolatus* Benth.; el de "New Spain" Herb. Pavón (G, F fragmento) a *L. minimiflorus* J. D. Smith, y los de *Oersted 2* (K) y *18* (K) a *L. orotinus* Pittier. Habiendo otro ejemplar de *Oersted 64* (K), el cual, por estar estéril no nos es posible precisar su identificación. En vista de lo anterior, al escoger al lectotipo se tomó en cuenta el como Bentham distinguió a este binomio de las especies afines que él disponía, así hace hincapié en lo ancho del fruto, y las pocas semillas que contiene, caracteres que corresponden a *L. orotinus* Pittier, el cual a su vez pasa a sinonimia, dado que se trata de un nombre posterior.

Aquí se ubica a *Lonchocarpus whitei* como sinónimo de *L. parviflorus*, ya que, el holotipo designado por Lundell en fruto corresponde a esta especie, el material (paratipos) en flor a *L. minimiflorus* J. D. Smith.

AESCHYNOMENEAE

Diphysa americana (Miller) M. Sousa, comb. nov. Basiónimo: *Colutea americana* Miller, Gard. Dict. ed. 8. *Colutea* No. 5. 1768. TIPO: México. Veracruz: (enviado en 1730), *W. Houstoun s.n.* (holotipo, BM).

Diphysa robinioides Benth. in Benth. et Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjoebenhavn. 1853. 11, 12. 1854. TIPO: Nicaragua: Volcán Mombacho, cerca de Granada, *A. S. Oersted 36* (lectotipo, K, aquí designado).

A pesar de que Bentham vió los ejemplares de Houstoun (están anotadas en puño y letra por él al pie de cada ejemplar) no usó el epiteto de Miller debido a que los identificó como *Diphysa carthagenensis* Jacq., error que hasta nuestros dias ha oscurecido la identidad de *Colutea americana*. En el Museo Británico existen dos ejemplares de W. Houstoun anotados como *Colutea americana*, pero P. Miller en su publicación aclara que se trata "del

enviado a él de Veracruz, en Nueva España, en el año de 1730." Así en tinta en manuscrito (no en máquina) su ejemplar tiene anotado "Vera Cruz, Houstoun 1730" y otro "e Vera Cruce 1731," siendo el primero el que consideramos al tipo, lo que es afortunado, ya que, se trata de un ejemplar con hojas, flores, y frutos; en cambio, el segundo está depauperado e inclusive su identidad específica es dudosa.

Miller (1768) citó a un polinomio de Plukenet *Colutea verae crucis vesicaria* (1692, tab. 165, fig. 3), sin basar su nombre en él, aunque si citándolo como la misma entidad, sin embargo como Britten & Baker (1897) ya nos aclararon, no se trata de lo mismo, es más la figura citada es una hoja de una mimosoidea, que pudiera ser un *Pithecellobium*. *Colutea americana*, como Miller nos informó, se basa en *Colutea americana, vesicules oblongis compressis* del manuscrito de Houstoun, además del material botánico traido a él en 1730.

Bentham identificó erróneamente al ejemplar de Seemann de Panamá (K) como *D. carthaginensis* [*carthagenensis*] Jacq., error que desde hace tiempo ha sido anotado por varios autores.

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A NEW COMBINATION IN *DIOCLEA* KUNTH (FABACEAE–DIOCLEINAE) FROM THE CLARIFICATION OF *D. GLABRA* BENTHAM, *FLORA BRASILIENSIS*[1]

Richard H. Maxwell[2]

Abstract

Comparing the *Dioclea glabra* collections cited by Bentham in *Flora Brasiliensis* in 1859, with the collections cited in his original descriptions of *D. glabra* and *D. coriacea* in 1837, reveals that the 1859 *D. glabra* collections include three species: *D. glabra* Benth. and *D. coriacea* Benth. (here lectotypified), and *D. scabra* (Rich.) Maxwell comb. nov. (here described and assigned a neotype). *Dioclea scabra* var. *brownii* and var. *schultzii*, both new varieties, are also described. The three species are placed in their appropriate sections.

In 1837 Bentham described 12 new species of *Dioclea*, including *D. glabra* and *D. coriacea*, and a new section, *Pachylobium* Bentham. Bentham's 1837 descriptions of *Dioclea glabra*, which he placed in sect. *Pachylobium*, and of *D. coriacea*, which he placed in sect. "*Eudioclea*" (sect. *Dioclea*), lacked descriptions of fruit characters.

When he described *Dioclea glabra* in *Flora Brasiliensis* in 1859, Bentham was able to include fruit characters from new collections. The 1859 description of *D. glabra*, however, contained elements of three separate taxa, *D. glabra*, *D. coriacea*, and *D. scabra*. He also moved *D. glabra* to his new sect. *Platylobium* Bentham and erroneously omitted *D. coriacea*.

My dissection of *Pohl 1578* (W), the lectotype of *Dioclea glabra* Benth. (1837), and study of Bentham's syntypes and other collections indicate that Bentham's original placement of *D. glabra* in sect. *Pachylobium* was correct, and that *D. coriacea* is in sect. *Platylobium* along with the new combination *D. scabra*. The invalidly published name *D. elliptica* Maxwell has been used in the literature (Kavanagh & Ferguson, 1981; van Roosmalen, 1985).

Key to Varieties of *Dioclea scabra*

1a. Leaflets with primary lateral veins in 6–8(–10) pairs, upper lamina mostly smooth.
  2a. Flowers 2.3–3 cm long ..... 1a. var. *scabra*
  2b. Flowers ca. 2 cm long ..... 1b. var. *brownii*
1b. Leaflets with primary lateral veins in 10–12 pairs, upper lamina rugose ..... 1c. var. *schulzii*

I. Dioclea scabra (Rich.) Maxwell, comb. nov.
TYPE: Guyana: Essequibo, Pomeroon River, 17–24 Dec. 1922, *J. S. de la Cruz 3090* (neotype, UC; isoneotypes, F, MO, NY, US).
Dolichos scaber Rich., Actes Soc. Hist. Nat. Paris 1: 111. 1792.

1a. **Dioclea scabra** var. **scabra.** Figure 1.

Nonsynonymous names applied to this species.

Dioclea glabra auct. div.: Pulle, Enum. 233. 1906; Huber, Bol. Mus. Paraense Hist. Nat. 4: 407. 1909; Ducke, Arch. Jard. Bot. Rio de Janeiro 1: 42. 1915, 4: 95, 330. 1925; Amshoff, Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 52: 69,70. 1939(a), Flora of Surinam 2: 204. 1939(b); Pittier, Bol. Técn. Minist. Agric. 5: 79. 1944; Maguire, Bull. Torrey Bot. Club 75: 395. 1948; Ducke, Bol. Técn. Inst. Agron. N. 18: 220. 1949; Cowan, Mem. New York Bot. Gard. 10: 150, 151. 1958; non Benth. 1837.

Dioclea elliptica Maxwell var. *elliptica*, nom. inval., *The Genus Dioclea (Fabaceae) in the New World.* Doctoral Dissertation. Southern Illinois Univ., Carbondale, Illinois. 1969. TYPE: Guyana: Essequibo, Pomeroon River, 17–24 Dec. 1922, *J. S. de la Cruz 3090* (holotype, UC; isotypes, F, MO, NY, US).

[1] I am grateful to the late Dr. Julian Steyermark for the opportunity to work on the *Flora of the Venezuelan Guayana*. The reviewers' helpful comments on nomenclature are acknowledged with gratitude. I also thank the directors and curators of A, BM, BRG, F, G, GH, GOET, IAN, K, MG, MO, NY, P, PORT, RB, S, SI, SIU, U, UC, US, and VEN for loans and, in many instances, hospitality in their herbaria. Thanks are due to Lewis Johnson for assistance with the illustration. A Grant-in-Aid of research from Indiana University Southeast is acknowledged.

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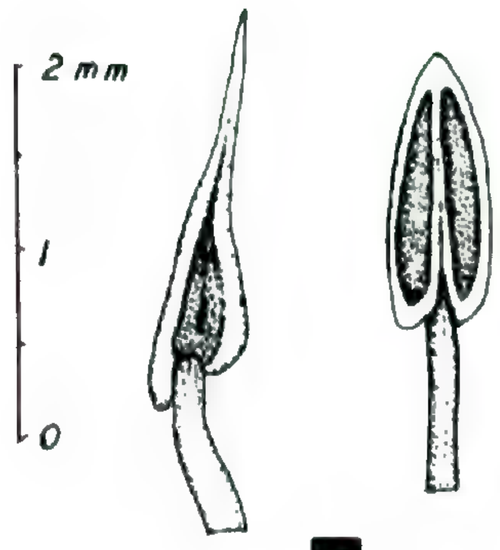
Lianas to 30 m tall, woody vines, or shrublets; stems terete, twining, occasionally with tendrils, usually glabrous, with raised, elliptic lenticels. *Leaves* trifoliate, the leaflets brittle or coriaceous, mostly elliptic, occasionally ovate or broadly lanceolate, 8–12(–24) × 4–9(–12) cm, the surfaces glabrous, the lower surface brownish, the apices mostly with elongate drip tips to ca. 2 cm long, the bases rounded, the primary lateral veins in 6–8(–10) pairs; petioles to ca. 10 cm long, the rachis ca. 2 cm long, both glabrous; stipules nonproduced, acute, to ca. 3 mm long, mostly persistent; stipels not seen, probably lacking. *Inflorescence* axillary, single, 20–50(–80) cm long, unbranched, ferruginous puberulent, becoming glabrate, flowering to ca. ½ its length, the rachis usually strongly angular, frequently with sections swollen and inhabited by ants; tubercles subsessile, the stalks stout, ascending, the heads incurved; bracts ovate, ca. 2 mm long, glabrous, semipersistent; bracteoles suborbicular to ovate, ca. 1.5 mm long, persistent. *Flowers* ca. 2.5 cm long, the pedicels 5–12 mm long, the calyx tube 7–12 mm long, sparsely ferruginous puberulent, the lobes 4, strongly upcurved, velutinous inside, the upper lobe obtuse, entire, ca. 6 × 10 mm, the lateral lobes falcate, acute to lanceolate, ca. 10 × 5 mm, the lower lobe lanceolate, ca. 12 mm long; standard reflexed, broadly oblong to somewhat orbicular, ca. 20 mm long with a claw ca. 5 mm long, entire or slightly emarginate apically, usually purple, lighter with age, bicallose, yellow or whitish in the center, somewhat carnose, glabrous; wings obliquely oblong to obovate, to ca. 15 × 10 mm with a claw 8 mm long; keels semiorbicular, to ca. 10 mm long with a claw 7 mm long, the upper margin basally auriculate, unlobed, the lower margin rising ca. 12 mm, culminating in a narrow or obtuse beak; stamens 10, pseudomonadelphous, the base of the vexillary free ca. 3 mm, mostly glabrous, the vexillary and inner alternate anthers of the staminal sheath imperfect, ca. 1.5 mm long, the 5 perfect anthers oblong, ca. 1.5–2.0 mm long; pistil geniculate or somewhat sigmoid, rising distally ca. 12 mm, the ovary ca. 7 mm long, short-stipitate, canescent villous, invariably 2-ovulate, the style with lower part hirsute, then swollen, somewhat triangular, narrowing to a flat, truncate apex, the upper part glabrous ca. 3.5 mm, the stigma subterminal. *Fruit* flat, twisting at dehiscence, dry, mostly obovate or oblanceolate, ca. 17 cm long, 2.2–3.0 cm wide basally to ca. 5 cm wide apically, the base rounded, the upper margin culminating in a short, downcurved beak, the exocarp mostly smooth, glabrate, the upper suture raised, with 2 close parallel ribs, the lower margin appearing flanged, 2-seeded; seeds flat, soft, dark, suborbicular, diameter 20–30 mm, 4–7 mm thick, the hilum oblong, 6–7 mm long.

Selected specimens examined. BRAZIL. AMAPÁ: Rio Oiapoque, *Irwin et al. 48038* (U, US); 2 km SE of Clevelândia, *Maguire et al. 47115* (NY, US). AMAZONAS: Rio Negro, between Manaus and São Gabriel, *Alencar et al. 358* (NY); *Black 48-2759* (NY, U, US, VEN); Manaus, *Chagas 356* (MG); 3 Feb. 1941, *Ducke 673* (F, MO, NY, SI, UC, US); 7 Dec. 1927, *Ducke RB 20423* (RB, S, U); Rio Cauaburi, *Holt & Blake 535* (K, NY, US); Rio Negro, *Kuhlmann 1030* (RB); Rio Negro, *Prance et al. 16007* (JEF, NY); Manaus, *Prance et al. 3178* (NY, S, US). PARÁ: Oriximiná, *Cid et al. 2469* (NY); Aramanahy, *da Costa 237* (F); Santarém, *Duarte 7231* (RB, SIU); Alto Tapajós, Missão Cururú, *Egler 825* (MG); Rio Arapiuns, *Pires & Silva 4394* (NY); Óbidos, Oct. 1850, *Spruce s.n.* (P), *Spruce 482* (P); Barra [= Manaus], June 1851, *Spruce 1643*[2] (P). FRENCH GUIANA: River Comté, *Aubréville 360* (US); Gourdonville, *Benoist 1514* (P); Cayenne, *L.C. Richard s.n.* (P); Sinnamary, route to Ste. Elie, *Sastre 6026* (US). GUYANA. ESSEQUIBO: Cuyuni River, *Aitken 1070* (S); Macouri Creek, *Archer 2487* (US); Essequibo River, *Atkinson 83* (BM); Kartabo, *Bailey 185* (GH); 4 mi. above Kaieteur Falls, *Cowan & Soderstrom 2090* (US); Pomeroon Dist., Pomeroon River, *de la Cruz 2972* (F, MO, NY, US); Potaro River at Tumatumari, *Gleason 330* (NY, US); Mazaruni River, *Jenman 625* (GOET, NY); Unabaruka Creek, *Martyn 223* (BRG, K); HMPS on Mazaruni Road, *Robertson & Austin 230* (MO); near Bartica, *Sandwith 129* (NY, RB). SURINAM: Toekoemoetoe Kreek, *Daniëls & Jonker 1336* (US); Kabalebo River, 20 km downstream from Kabalebo airstrip, *Florschütz & Maas 2589* (F, U); Lucie River, *Irwin et al. 55379* (F, GH, MO, NY, U, US, VEN); Saramacca River, *Maguire 24070* (F, U, US); *Pulle 203* (U); Lihanie River, *Rombouts 717* (NY, U); Lawa River, *Versteeg 274* (U); Upper Litanie River, *Versteeg 401* (U); Tapanahoni River, *Versteeg 662* (U). VENEZUELA. AMAZONAS: Cerro de La Neblina, Río Mawarinuma, *Anderson 13337* (NY); km 11 NE of San Carlos de Río Negro, *Davidse & Miller 26536* (MO, NY); 0 to 0.5 km SE of San Carlos de Río Negro, *Liesner 4019* (JEF, MO); Río Cunucunuma, *Maguire et al. 29498* (NY); Alto Orinoco, *Ll. Williams 15235* (F, VEN); forest of Orinoco, Esmeralda, *Ll. Williams 15510* (G, US, VEN); Casiquiare River, *Ll. Williams 15672* (F, US, VEN); Río Orinoco, frequent just above Tama-Tama, *Wurdack & Adderley 43113* (GH, NY, US, VEN). BOLÍVAR: Reserva Forestal Imataca, *Stergios et al. 2769* (PORT).

1b. Dioclea scabra var. **brownii** Maxwell, var. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Atabapo, SE bank of middle part of the Caño Yagua at Cucurital de Yagua, 8 May 1979, *Davidse et al. 17450* (holotype, MO; isotypes, MYF n.v., NY).

Flores ca. 2 cm longi; pedicellis ca. 4 mm longis; vexillo obovato-orbiculari, valde bicalloso; vexillari filo pubescenti ad basem. Legumen ignotum.

Leaflets elliptic, 9–12 × ca. 5 cm, both sides dull, glabrous; petioles and rachis glabrous. *Flowers*



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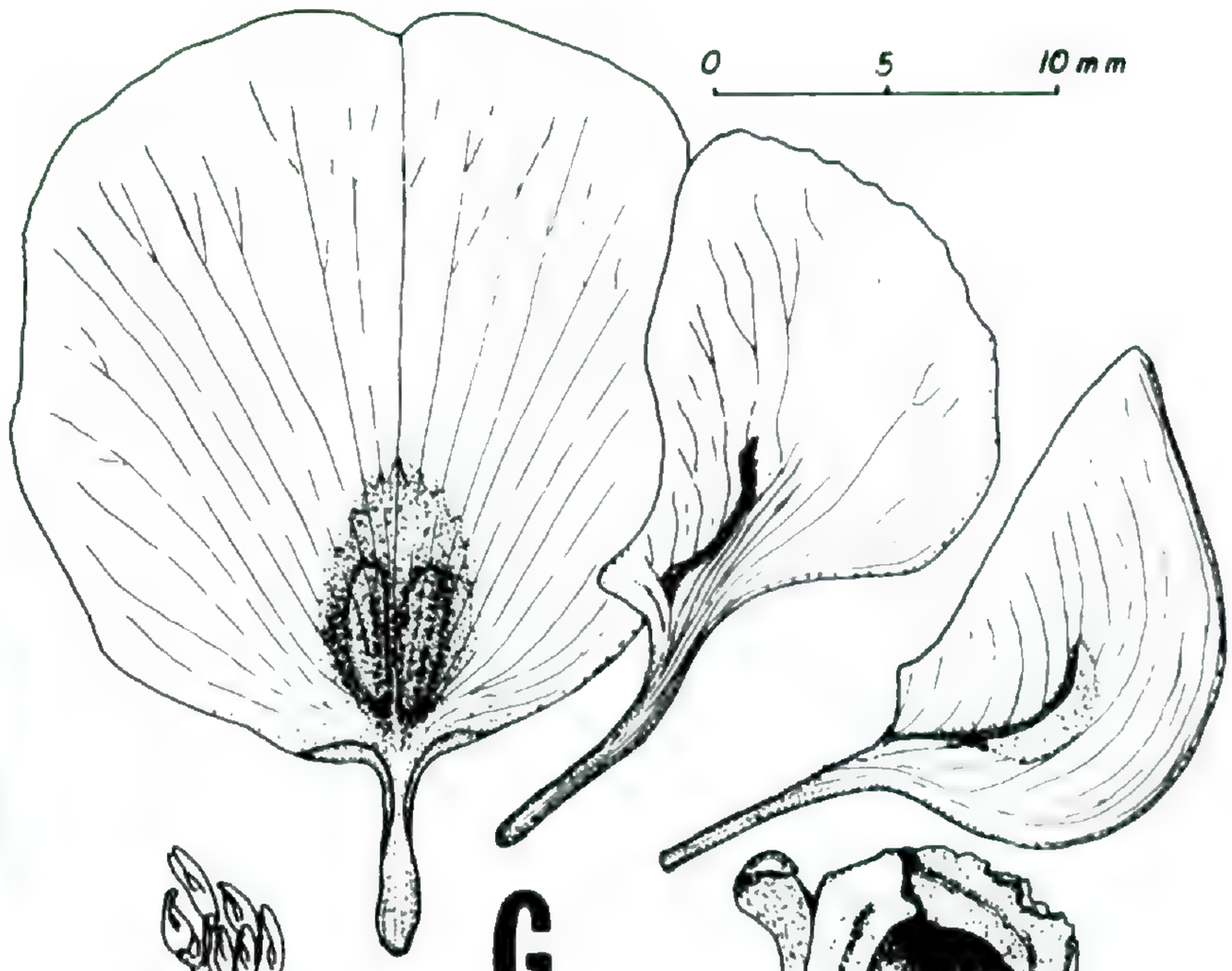

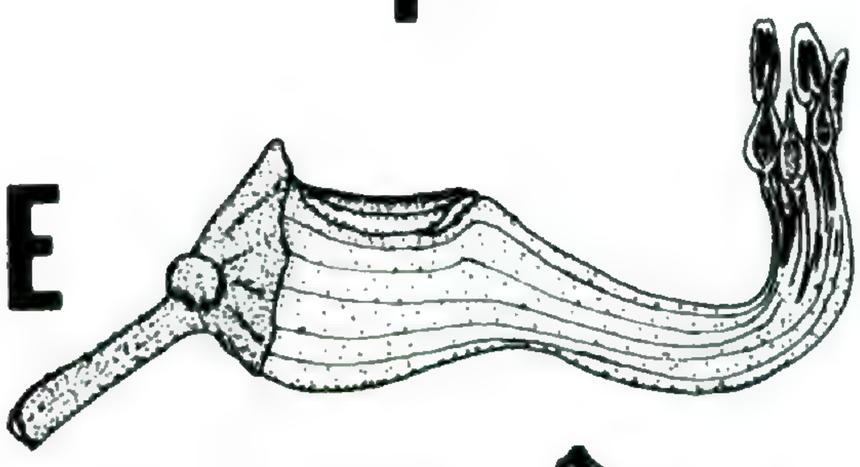

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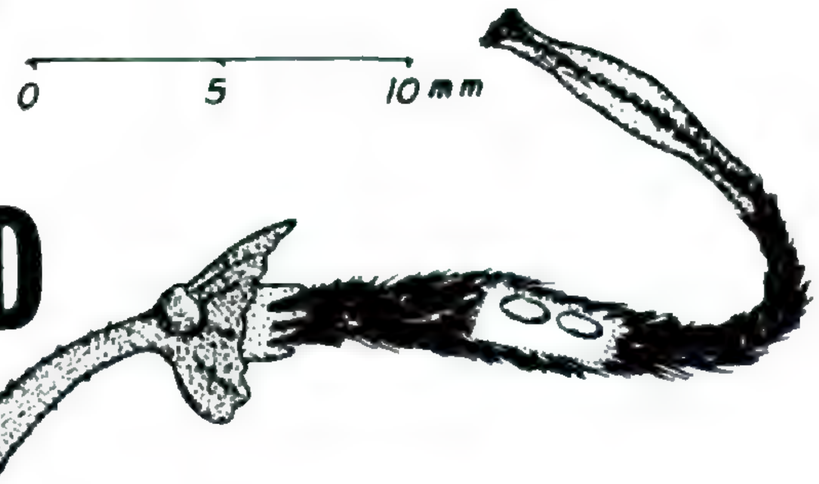

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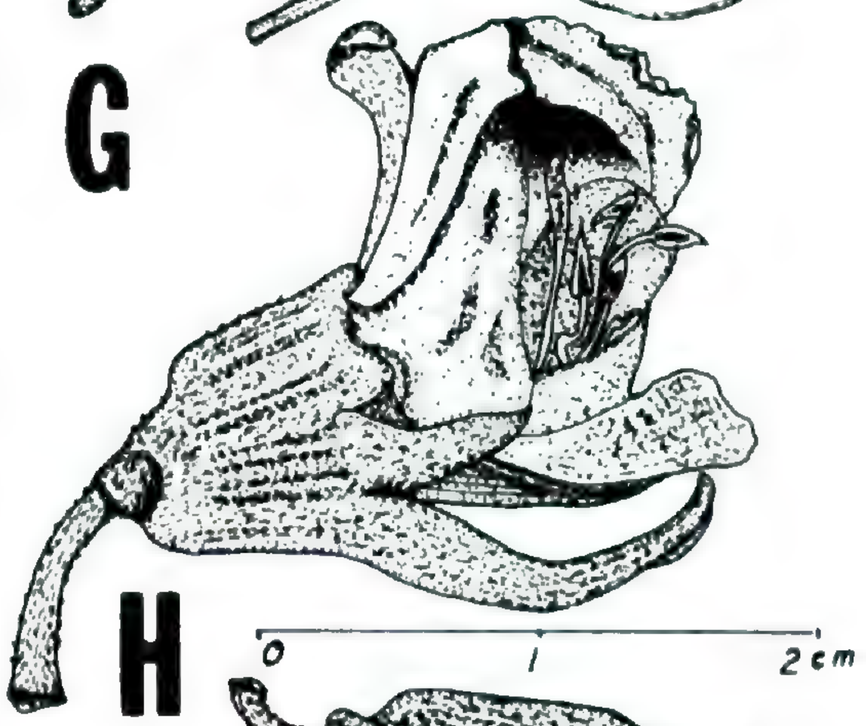

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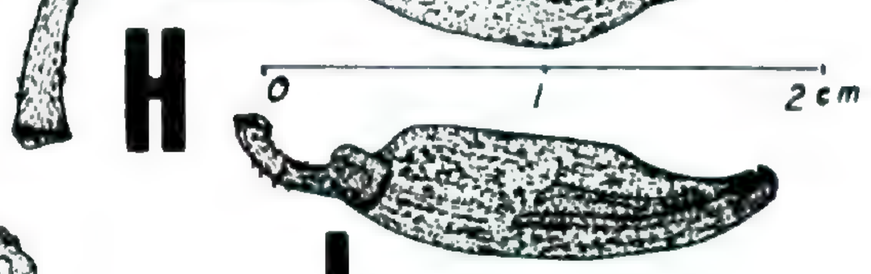

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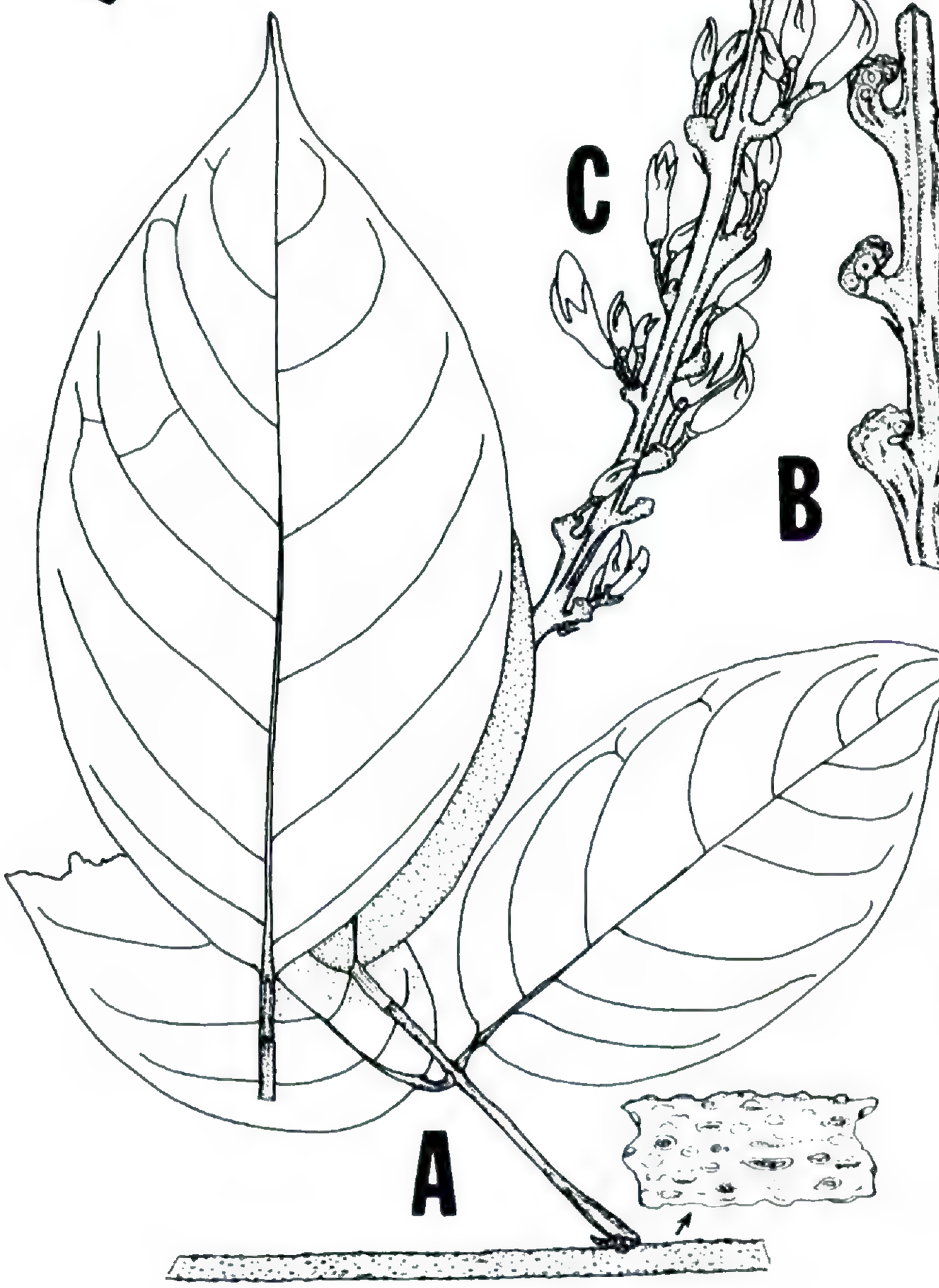

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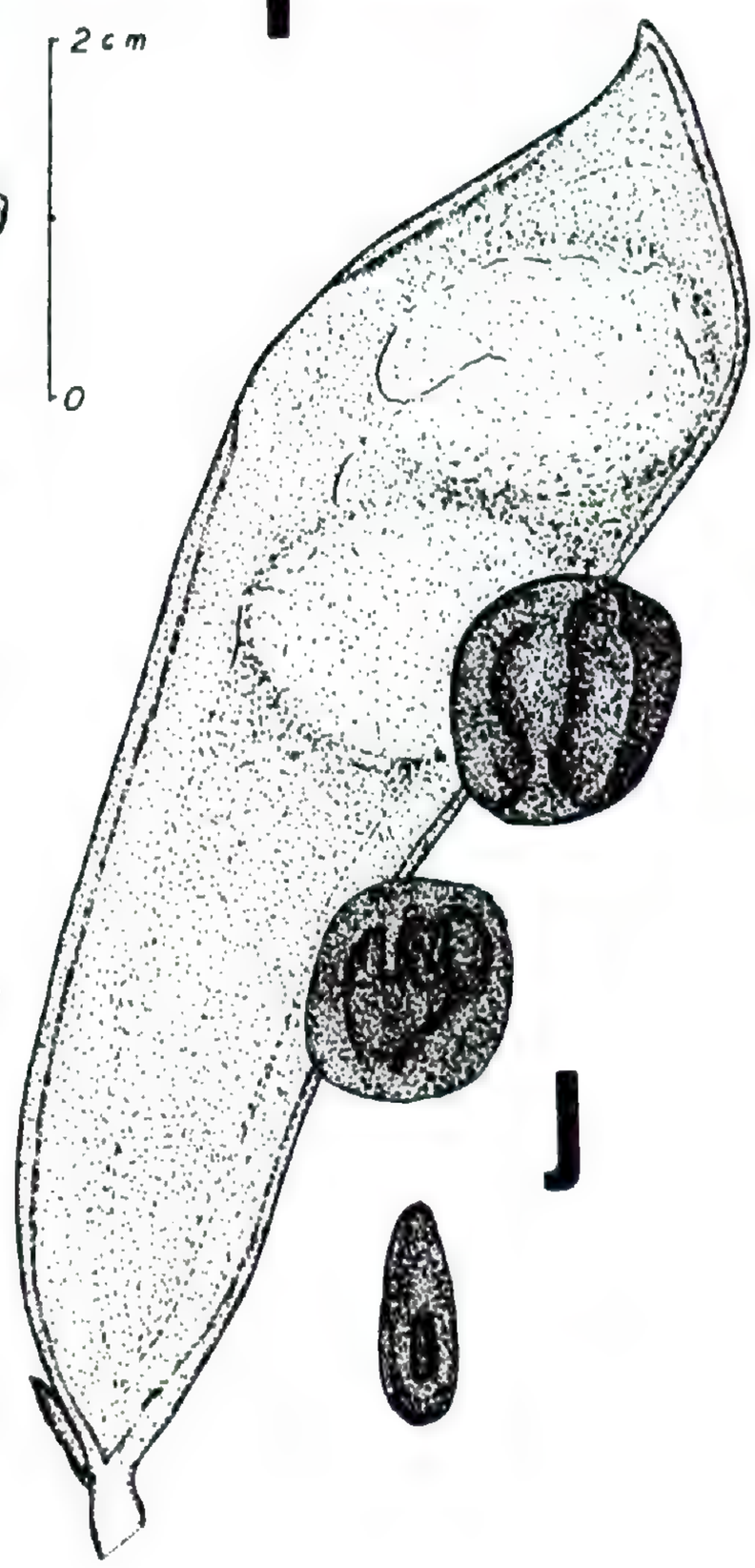

J

to ca. 2 cm long, the pedicels ca. 4 mm long, the calyx tube ca. 6 mm long, the lobes slightly upcurved, the upper shallowly bifid or entire; standard obovate-orbicular, strongly reflexed, bicallose; anthers dimorphic, the base of the vexillary stamen pubescent; pistil deeply bent, almost sigmoid. *Fruit* unknown.

This variety shows some characters of *Dioclea ruddiae* Maxwell and *D. macrocarpa* Huber, but androecium and gynoecium characters are shared with *D. scabra*. I expect fruit and seed to be similar to var. *scabra* but smaller. Known from type locality only.

I am naming this variety after H. E. Brown, who realized that Bentham's *Dioclea glabra* of 1859 was not the same as Bentham's *D. glabra* of 1837. Brown wrote on an envelope affixed to *Gleason 330* [var. *scabra*] (NY), "This species = Jenman 625 [var. *scabra*] & 984 [n.v.] and unnumbered specimen of Schomburgk [n.v.] which have been named *Dioclea glabra* Benth. But (as I noted in the herbarium in 1880) it is quite distinct from Bentham's type of *D. glabra* and requires a new name."

1c. Dioclea scabra var. **schulzii** Maxwell, var. nov. TYPE: Guyana: Essequibo, Potaro, brown tough rope from crown of tree in Kakaralli clump Wallaba forest on red laterite soil, 7 Mar. 1949, *Atkinson 116* (holotype, BM; isotypes, NY, US). Record No. 6025, Forest Dept. No. 2878. ["D. B. Fanshawe" is on the NY sheet.]

Foliola elliptica, infra manifeste reticulata, glabrata, supra rugosissima, glabra, abrupte acuminatis apicibus ca. 2.5 cm longis, 10–12 venis; stipulis lanceolatis.

Leaflets elliptic, distinctly reticulate below becoming glabrate, strongly rugose above, glabrous, the apices abruptly acuminate, the drip tips about 2.5 cm long, the primary lateral veins in 10–12 pairs; stipules lanceolate, mostly exceeding 6 mm.

Known from the type locality only. Named after J.P. Schulz (Dienst's Lands Bosbeheer, Surinam (1968)). This variety is similar in flower characters (and I assume fruit) to var. *scabra*.

DISCUSSION AND LECTOTYPIFICATIONS

Bentham's new sect. *Pachylobium* of 1837 included *Dioclea glabra* Benth., which is lectotypified here.

Dioclea glabra Benth., Comm. Legum. Gen.: 69. 1837. TYPE: Brazil. Goiás (?): ad San Izidro, *Pohl 1578* (lectotype, W, photo at M, F neg. no. 32009); ad San Izidro, *Pohl s.n.* (isolectotype? K, photo F, photo S of questionable isolectotype at K, NY photo neg. series 2479).

Of the syntypes cited by Bentham, I believe "Ad San Izidro" *Pohl s.n.* is *Pohl 1578* (W) and the collection number was added later. I selected *Pohl 1578* (W) as lectotype because of notations (especially concerning localities) on the herbarium sheets, the preservation of Bentham's original intent in 1837 as to section placement and description, and the type photos in current usage.

My dissection of *Pohl 1578* (W), the lectotype of *Dioclea glabra* Benth. (1837), revealed 8–9 ovules and calyx characters that do not fit Bentham's sect. *Platylobium*. Study of *D. glabra* seed characters, especially the linear, half-encircling hilum, indicates the original placement in sect. *Pachylobium* was correct. In 1859 Bentham described sect. *Pachylobium* as having 2–3 (rarely 4) ovules. I believe the number of ovules in this section is much more variable.

Bentham's 1837 sect. "*Eudioclea*" [sect. *Dioclea*] included *Dioclea coriacea* Benth., which is lectotypified here.

Dioclea coriacea Benth., Comm. Legum. Gen. 69. 1837. TYPE: Brazil. Amazonas: Goiás: Congo do Padre, *Pohl 1996* (lectotype, W); Congo do Padre, Herb. Mus. Vind. 1837, *Pohl s.n.* (isolectotypes?, K, NY, photo of NY specimen at S, photo of K specimen at US, NY photo neg. series 2480).

Of the syntypes cited by Bentham, I believe the "Congo do Padre" *Pohl s.n.* is *Pohl 1996* (W). I selected *Pohl 1996* (W) as lectotype because no-

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FIGURE 1. *Dioclea scabra* var. *scabra*.—A. Leaflets, part of stem (*Prance et al. 16007*, JEF).—B. Inflorescence rachis section with tubercles and bracts (*Prance et al. 16007*, JEF).—C. Inflorescence section (*Liesner 4019*, MO).—D. Pistil showing ovule positions (*Prance et al. 3178*, S).—E. Staminal sheath with pseudomonadelphous stamens (*Wurdack & Adderley 43113*, VEN).—F. Dimorphic anthers (*Wurdack & Adderley 43113*, VEN).—G. Petals: standard, wing, and keel (*Wurdack & Adderley 43113*, VEN).—H. Flower (*Irwin et al. 55379*, VEN).—I. Flower bud (*Irwin et al. 55379*, VEN).—J. Fruit, 2-seeded (*Ll. Williams 15672*, VEN); seeds (*Ducke, 7-12-1927, RB No. 20423*, RB).

tations (including "tipse") on the herbarium sheet, and the accurate type photos of the presumed isolectotype at K.

I believe Bentham's other *Dioclea coriacea* syntypes (1837) included heterogeneous elements, which I have determined as follows: Ega Amazonum, *Pöppig* [= *Pöppig 2886*] (paratype? W, 3 sheets with very immature inflorescences = *D. coriacea* or *D. macrocarpa* Huber?); In margine sylvarum prope Para, *Martius* [= *Martius 2716*] (M) = *D. glabra* sensu Bentham (1837).

Bentham's 1859 description of *Dioclea glabra* in *Flora Brasiliensis* is based on the following collections: "Habitat in silvis prov. Paraënsis, Piauhiensis et do Alto Amazonas: M[artius], Spruce: in prov. Pernambucensi: *Gardner n. 2823.*; in prov. Goyazensi: Pohl; et in prov. Mato Grosso secus flumen Paraguay: Weddell." I have sorted out these *Flora Brasiliensis* collections into three separate taxa as follows. The *Martius* collections (M) are paratypes of *D. glabra* (1837). The *Spruce* collections, Barra do Rio Negro, June 1851, *Spruce 1643*[2] (P); Óbidos, *Spruce s.n.* (P) are *D. scabra*. *Spruce 1139* (M), San Gabriel da Cachoeira, Rio Negro, Jan., Aug. 1852, is *D. glabra*? Of the *Spruce* collections from between Santarém and Barra do Rio Negro, Oct. 1850, *Spruce s.n.* (W) is *D. coriacea*; Oct. 1850, *Spruce 1190* (M) is *D. glabra* (1837). *Gardner 2823* (BM, K) is *D. coriacea*. The *Weddell* collections from Paraguay R., *Weddell 3269* (F, P); April–May 1845, *Weddell 3269* (P), 1848, *Weddell 3269* (P) are all *D. glabra* Benth., sensu 1837. Again, I believe the number "3269" was added later.

Bentham's 1859 citation "in prov. Goyazensi: *Pohl*;" is I believe "ad S. Izidro" *Pohl 1578* (W), the lectotype of *Dioclea glabra* Benth. (1837). The other "ad S. Izidro; *Pohl*" citation in *Flora Brasiliensis* is *Dioclea latifolia* Benth., but the type is unequivocal as Bentham (1837) cited only one collection, *Pohl 1565* (K, W). Pohl's itinerary included "Corgo (*sic*) do Padre" in Goiás, according to Urban (1906), and it is possible Bentham included the lectotype of *D. coriacea* (1837) among the collections under *D. glabra* (1859), although *D. coriacea* was not cited in synonymy.

Bentham (1859) also gave a northern distribution for *Dioclea glabra*, "Crescit etiam in Guyana anglica et gallica." However, *D. glabra*, sensu 1837, has never been found in Guyana or French Guiana; this part of Bentham's distribution refers to *D. scabra*.

Pulle (1906) followed the concept of *Dioclea glabra* as used in the *Flora Brasiliensis*. Huber (1909) noted discrepancies between specimens determined *D. glabra* and Bentham's description in *Flora Brasiliensis*. Work by Ducke (1915, 1925a, b) on the Amazonian flora established the concept of *D. glabra* in sect. *Platylobium* rather than sect. *Pachylobium*, at least in the New World. Ducke described *D. leiophylla* in sect. *Pachylobium* in 1925a, and I (1969) placed that binomial in synonymy under *D. glabra* Benth., sensu Bentham (1837); this treatment was followed by Lewis (1987). Pittier (1944) also noted that Bentham's 1859 calyx and fruit description of *D. glabra* did not match the common *D. glabra* (= *D. scabra*) of Esmeralda, Alto Orinoco, Venezuela. *Dioclea coriacea* Benth. became lost in Ducke's (1925, 1949) "forms" of *D. glabra* and *D. bicolor* Benth.

Amshoff (1939a) cited Richard's description (1792) of *Dolichos scaber* and noted, "When this is really a *Dioclea* species, the description agrees very well with *D. glabra* Benth." This was *D. glabra* Benth., sensu 1859 (= *D. scabra*).

Amshoff (1939a) further stated that no specimens determined *Dolichos scaber* could be traced in the Paris herbarium. Amshoff (1939b) in Pulle's *Flora of Surinam* added under *Dioclea glabra*, "— vs. *Dolichos scaber* . . ." indicating she might have seen dried specimens.

New species described by L. C. Richard (1792) were based on specimens collected by Leblond in Cayenne and are now housed at G according to Stafleu & Cowan (1983). A search for the type of *Dolichos scaber* was undertaken by Dr. A. Charpin at Geneva. A holotype was not found in G and G-DC collections. Article 37 of the *International Code of Botanical Nomenclature* (1988) states citation of a type is not necessary prior to 1958. However, since no types have been found and Richard's description (1792) was extremely brief, I have selected *J. S. de la Cruz 3090* as the neotype.

I have taken up the epithet *scabra* as a valid name and have placed *Dioclea elliptica* in synonymy.

The three taxa, *Dioclea glabra*, *D. coriacea*, and *D. scabra*, more or less share Bentham's description of small, nonproduced (probably lacking in *D. glabra*) stipules, an overall glabrous aspect, as well as ovate or elliptic, coriaceous leaflets. However, *D. glabra* Benth. (1837) is a sizable liana distributed throughout the southern Amazonian region of Brazil and farther south along the rivers and gallery forests into the planalto and Mato Grosso. It is often collected. The fruit was illustrated by Ducke (1925a, pl. 5) as *D. leiophylla*.

Dioclea scabra, the northernmost element of sect. *Platylobium*, is found in Amazonas and Bo-

lívar of the Venezuelan Guayana, the Guianas, and in Amapá, Pará, and Amazonas in Brazil. *Dioclea coriacea* is sympatric with *D. scabra* to the north, but extends farther south in Brazil into the planalto and campos. Both grow as vines or shrublets.

Dioclea scabra differs from *D. coriacea* by possessing a stout, ridged peduncle and rachis, ascending stout tubercles, larger flowers, sharply upturned calyx lobes, the lower lobe tip hooked or cupped over the upper lobe in the bud, standard broadly oblong to somewhat orbicular, and larger fruit.

In contrast, *Dioclea coriacea* has a slender inflorescence, long-stalked tubercles extending out from the rachis, smaller flowers, the largest to ca. 2.3 cm long, calyx lobes somewhat straight or the lower lobe upturned, standard mostly obovate, and smaller fruit, the largest to ca. 12 cm long, 3 cm wide basally to ca. 4 cm wide apically.

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NOTES

NEW TAXA OF *DIOCLEA* KUNTH (FABACEAE–DIOCLEINAE) FROM THE VENEZUELAN GUAYANA

Study of new collections and reexamination of old collections for the *Flora of the Venezuelan Guayana* have necessitated the validation of names for three taxa.

Dioclea sect. *Dioclea* [sect. *Eudioclea* Benth. (1837)]

1. Dioclea holtiana Maxwell, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Boca del Vichada, 13 Jan. 1930, *Holt & Gehriger 224* (holotype, US; isotype, VEN). [*Dioclea holtiana* Pittier, Bol. Técn. Minist. Agric. No. 5: 84, fig. 36. 1944, nom. inval. publ. sine descr. latin. Based on: Venezuela. Territorio Federal Amazonas: Boca del Vichada, Alto Orinoco, *Holt & Gehriger 240* (VEN n.v.).]

Foliola elliptica-ovata, vel late lanceolata. Inflorescentiae 40–60 cm longae. Flores 2.5–3.0 cm longi; bracteolis parvis, acutis, caducis; calycis tubo pubescenti, calycis supero lobo tubum multo superanti; vexillo elliptico-oblongo, emarginato; alis sine calcari. Ovarium ca. 10-ovulatum.

Vines, climbing in thickets and woods; stems terete, with erect, velutinous, rufous or somewhat canescent pubescence. *Leaves* trifoliolate; leaflets oval, elliptic-ovate or broadly lanceolate, 4.0–8.5 × (1–)2.5–5.0 cm, the upper surface sparsely pubescent, dense along the midrib, the lower surface villous with diffuse somewhat curly pubescence, the apices mostly obtuse, occasionally acute or rounded, the bases oblique, mostly rounded, occasionally cuneate or slightly cordate, the primary lateral veins in ca. 7 pairs; petioles 2.5–4.5 cm long, the rachis 1–3(–9) mm long, this, petiole, and pulvinules with dense erect pubescence; stipules not produced below insertion, lanceolate, ca. 2.5 mm long, caducous?; stipels setaceous, 1–2 mm long, apparently persistent. *Inflorescences* axillary, single, 40–60 cm long, with appressed, ascending, short pubescence, flowering to ca. ½ its length; tubercles clavate or somewhat elongate, the lower occasionally long-stalked, the nodes distant; bracts lanceolate, ca. 2.5 mm long, mostly persistent; bracteoles ovate, ca. 2 mm long, caducous; pedicels 3–5 mm long. *Flowers* 2.5–3.0 cm long, the buds straight or slightly downcurved, the calyx tube ca. 6 mm long, sparsely pubescent, canescent velutinous inside, the upper lobe lanceolate, entire, ca. 10 mm long, entire, the lateral lobes 6–8 mm long, the lower lobe somewhat linear-lanceolate, ca. 10 mm long; petals with claws ca. 4 mm long, the standard reflexed, elliptic-oblong, emarginate, ca. 20 × 14 mm, the wings oblanceolate, ca. 23 × 8 mm, the auricle sharp-pointed, without a spur, the keels obliquely oblong or somewhat oblanceolate, 16 × 6 mm, weakly auriculate, the upper middle margin serrate; stamens 10, glabrous, pseudomonadelphous, the anthers perfect; pistil straight for ca. 16 mm then geniculate, rising distally ca. 5 mm, the ovary ca. 10 mm long, short-stipitate, with a disc collar, ca. 10-ovulate, canescent villous; style uniform, distally glabrous ca. 8 mm; stigma terminal, capitate. *Fruit* compressed, oblong, straight or slightly downcurved, to ca. 11.0 × 1.5 cm, dehiscent, the exocarp with appressed, white to ferruginous pubescence, the upper suture with a shallow parallel rib ca. 1.5 mm on each side, the lower suture lacking ribs, 8–11-seeded; seeds hard, oval or ellipsoid, to ca. 9 × 6 × 2 mm, the hilum linear, ca. 7 mm long.

Additional specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Atures, cuenca del Río Cataniapo, *Guanches 1555* (MO); Atures, alrededores de Puerto Ayacucho, *Huber 1335* (US), *Huber & Cerda 1448* (US), *Stergios 3225* (PORT).

Pittier in 1945 again cited *Holt & Gehriger 240* as the *Dioclea holtiana* type. My selection of the type is based on the assumption that Killip at US selected *Holt & Gehriger 244* as the type with Pittier's knowledge. Pittier corresponded with Killip during this period regarding *Dioclea*. Many VEN herbarium collections of *Dioclea* have invalid

names written on the genus covers. "*Tipo*" is written on several sheets with these same names. There are sheets with illustrations of floral dissections attached, probably indicating intended publication and certainly indicating that Pittier's work was left unfinished. Few of these names warrant species rank, but *D. holtiana* is an exception.

The Guayana collections cited date from 8 December to 26 January. Collectors report the calyx dark purple or dark red-purple with the corolla rose-whitish, pallid purple, blue-purple to whitish, or white.

Collectors further report the species common in fields, woods, and thickets, from 90 to 150 m altitude. Flowers of the cited Guayana specimens are similar to those of the closely related *Dioclea albiflora* Cowan (1958). *Dioclea albiflora* has leaflets with denser pubescence, longer flowers, short-clawed wings with spurs, somewhat oblong keels, thinner fruits, and an almost-glabrous calyx except for the upper and lower midribs. While I consider *D. albiflora* a restricted Guayana endemic, *D. holtiana* ranges from Guayana into Vichada, Colombia, and north into other Venezuelan states.

Dioclea virgata (Rich.) Amshoff, On South American Papilionaceae. Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 52: 69. 1939.

2. Dioclea virgata (Rich.) Amshoff var. **crenata** Maxwell, var. nov. TYPE: Brazil. Amapá: region of Calçoene, Calçoene River, coastal region, creeping liana, frequent in shrubby savanna, 20 Aug. 1962, *Pires & Cavalcante 52528* (holotype, U; isotypes, NY, SP, US).

Flores ca. 2–3 cm longi; bracteolis ca. 6 × 4 mm; supero, medio margine carinae minute crenato vel dentato. Legumen pubescentia persistenti, canescenti, velutina vel tomentosa.

Stems twining, climbing. *Leaflets* mostly ovate, occasionally broadly lanceolate to elliptic, 6–11.5 × 3.5–5.5 cm, sparsely pubescent above and below, the apices abruptly acute or somewhat acuminate, the bases rounded to somewhat cordate, the primary lateral veins in ca. 7 pairs; petioles 2.5–4 cm long, the rachis to ca. 2 mm, this and petiole sparsely pubescent; stipules not produced; stipels setaceous. *Inflorescences* axillary or terminal, usually single, long, sparsely pubescent; tubercles mostly elongate, upcurved; bracts acute, persistent; bracteoles oval or orbicular, ca. 6 × 4 mm, occasionally larger; pedicels ca. 5 mm long. *Flowers* 2–3 cm long; keels nearly oblong, the upper middle margin usually with ca. 5 shallow dentate or crenate teeth, the wings obliquely obovate, usually without a spur; stamens 10, anthers perfect; pistil usually somewhat sigmoid, the ovary canescent. *Fruit* canescent pubescent, nearly tomentose, lanate or erect-velutinous.

Additional specimens examined. BRAZIL. AMAPÁ: coastal region, *Pires & Cavalcante 51998* (NY, RB, VEN), *52026* (NY). AMAZONAS: Barcelos, *A.P. Duarte 7239* (SIU); vicinity of Santarém, *Ginzberger s.n.* (W). PARÁ: Oriximiná, Rio Paru do Oeste, *Cid et al. 2306* (NY); Oriximiná, 17 Sep. 1910, *Ducke MG 10996* (BM); Montealegre, 24 Apr. 1916, *Ducke MG 16048* (BM, RB); Santarém, *Silva & Souza 2213* (NY). SURINAM: Saramacca River, *Pulle 98* (U). VENEZUELA. AMAZONAS: *Ll. Williams 14536* (US, VEN); Dept. Río Negro, *Stergios & Aymard 4164* (PORT); Bajo Casiquiare, *Stergios & Aymard 7328* (MO); Río Casiquiare, *Stergios et al. 9772* (JEF, PORT).

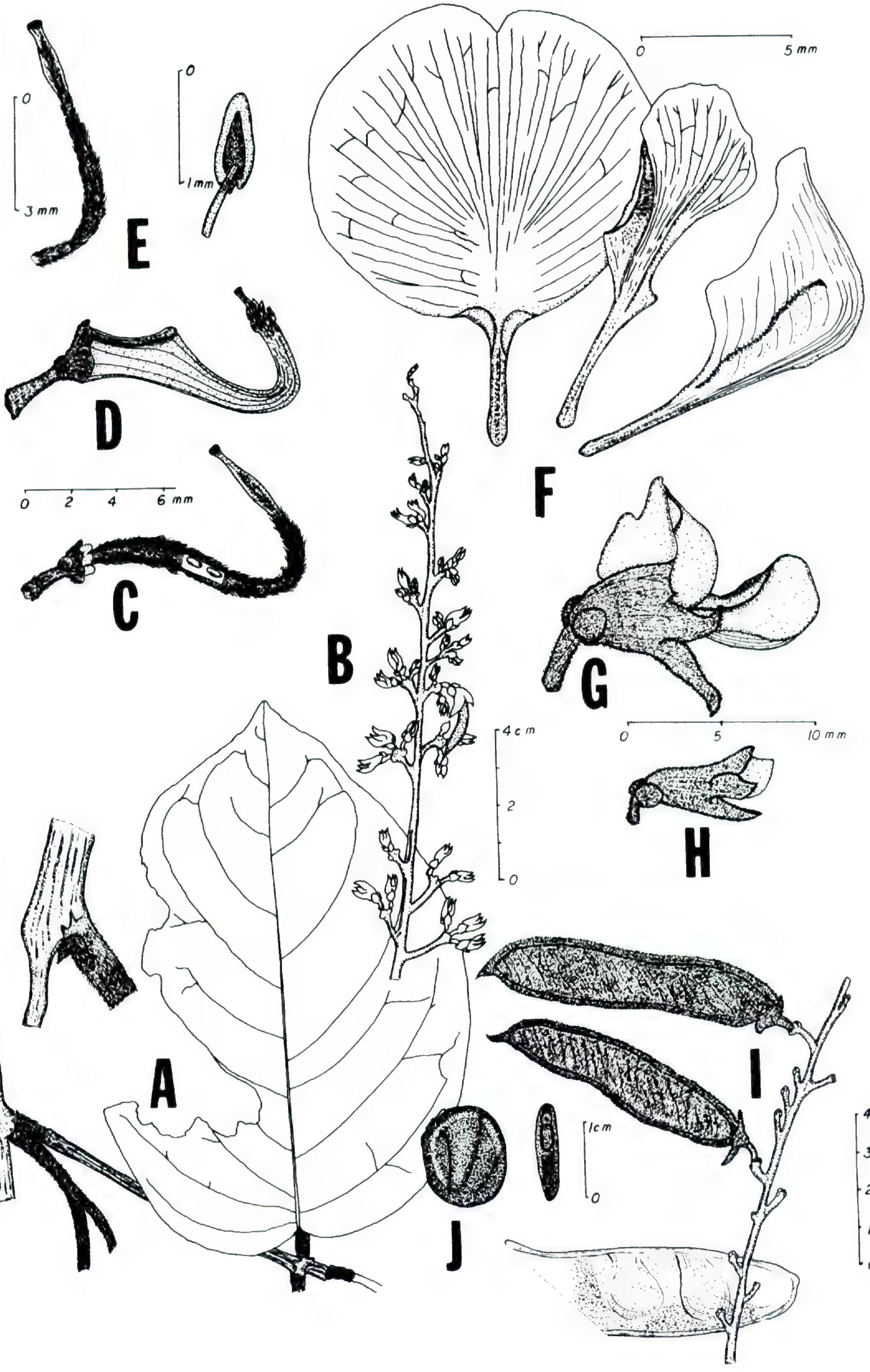
Dioclea virgata var. *crenata* is separated from var. *virgata* by having smaller flowers, pedicels, and bracteoles, and the keels lack fimbriations, and the fruit exocarp has short (mostly canescent) pubescence rather than the stiff, erect ferruginous hairs of var. *virgata*. An excellent illustration of var. *virgata* is found in the *Flora Brasiliensis* (plate 44, as *Dioclea lasiocarpa* Mart. ex Benth.).

Dioclea aff. sect. *Macrocarpon* Amshoff, On South American Papilionaceae. Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 52: 69. 1939.

3. Dioclea steyermarkii Maxwell, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Atures, 5°21′N, 66°15′W, 550 m, savannas, situated in a region of hills and ridges S and SE of Cerro Camani, *Huber 4476* (holotype, US; isotypes, MYF n.v., NY). Figure 1.

Frutex ad ca. 1 m altus vel scandens. Foliola rigida-coriacea, lanceolata-ovata-elliptica, ad 14 × 10 cm, sparse pubescentia, stipulis non productis. Inflorescentiae axillares, ad 60 cm longae; tuberculis clavatis; bracteolis ovatis, ca. 2 × 1.5 mm, persistentibus. Flores ad 1.5 cm longi, calycis lobis tubum quasi aequantibus; vexillo orbiculari-ovato; alis oblanceolatis cum calcaribus; carinis triangularibus.

Vines or shrublets, to 1 m tall; stems terete, glabrescent. *Leaves* trifoliolate, the leaflets rigid coriaceous, the lamina elliptic to broadly ovate, to ca. 14 × 10 cm, the upper surface glabrous, the lower surface glabrescent, the apices rounded, then abruptly acute, the bases somewhat rounded to cordate, the primary lateral veins in 7–9 pairs; rachis and petioles sparsely pubescent; stipules acute-acuminate, not produced below insertion, ca. 4 mm long; stipels not seen. *Inflorescences* axillary or terminal, single, to ca. 60 cm long, mostly ferruginous tomentose, becoming glabrescent, flow-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ering for ¾ or more of their lengths; tubercles long-stalked, each ca. 5-flowered; bracts not seen; bracteoles ovate, ca. 2 × 1.5 mm, persistent; pedicels ca. 2–3 mm long. *Flowers* to 1.5 cm long, usually smaller, the buds ± straight, the calyx tube to ca. 6 mm long, sparsely pubescent, sericeous inside extending up the lobes, the upper lobe obtuse, entire, the lower lobe longest, lanceolate, 5–7 mm long; petals with claws ca. 5 mm long, the standard strongly reflexed, orbicular or broadly ovate, 10 × 12 mm, the wings oblanceolate to obliquely oblong, longer than the keels, 7 × 5 mm, usually with a spur, the keels triangular to obliquely oblong, 7 × 6 mm, the upper margin basally auriculate, entire, the beak obtuse or slightly outcurved; stamens 10, pseudomonadelphous, the base of the vexillary filament free ca. 2 mm, the anthers perfect; pistil somewhat sigmoidal, the ovary ca. 4 mm long, substipitate, hirsute, 2–4-ovulate; style glabrous distally ca. 5 mm, swollen; stigma apparently terminal. *Fruit* oblong to oblanceolate, compressed, ca. 9 cm long, ca. 1 cm wide proximally to ca. 2.6 cm distally, dehiscent, the exocarp densely ferruginous pubescent, 2–4-seeded; seeds ovoid, smooth, ca. 14 × 13 × 3.5 mm, the hilum oblong, ca. 4 mm long.

Additional specimen examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: savannas, basin of Río Manapiare, *Huber 1201* (NY, US).

The ten perfect anthers and the oblong fruit with seeds evenly distributed suggest placing this species in sect. *Macrocarpon*; however, the habit and general characteristics show a close affinity to *Dioclea coriacea* Benth. (1837) of sect. *Platylobium* Benth. (1859). *Dioclea coriacea* has the five perfect plus five imperfect anthers and is invariably two-ovulate, producing an oblanceolate, two-seeded fruit.

This species is named in honor of the late Dr. Julian Steyermark.

I thank Dan H. Nicolson and Velva E. Rudd for helpful comments. I also thank Lewis Johnson for assistance with the illustration. For the opportunity to study *Dioclea* material, I thank the directors and curators of the following herbaria: BM, MO, NY, PORT, RB, SIU, SP, U, US, VEN, and W.

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FIGURE 1. *Dioclea steyermarkii.*—A. Leaflet attached to stem, *Huber 4476* (NY).—B. Upper portion of inflorescence, *Huber 4476* (NY).—C. Pistil showing positions of ovules, *Huber 1201* (NY).—D. Staminal sheath with pseudomonadelphous stamens, *Huber 1201* (NY).—E. Stigma, upper style, and anther, *Huber 1201* (NY).—F. Petals: standard, wing, and keel, *Huber 4476* (NY).—G. Flower, *Huber 4476* (US).—H. Flower bud, *Huber 4476* (US).—I. Portion of inflorescence with fruit and interior of mature fruit, *Huber 1201* (NY).—J. Seeds, *Huber 1201* (NY).

NOTES AND NEW COMBINATIONS IN HAWAIIAN *PANICUM* (POACEAE: PANICEAE)

The genus *Panicum* (excluding *Dichanthelium* sensu Clark & Gould, 1978) is quite diverse in the Hawaiian Islands, with 11 native species (five perennial, six annual) recognized by me in the account of the genus for the *Manual of the Flowering Plants of Hawaii*. Hitchcock (1922) also recognized 11 species, but the circumscriptions in my account differ from those of Hitchcock for many of the species.

St. John (1987) published 20 new species and one new variety while my account was in press. This included two later homonyms: *P. furtivum* St. John, Phytologia 63: 369. 1987, non Swallen, Contr. U.S. Natl. Herb. 29: 421. 1950; and *P. simplex* St. John, Phytologia 63: 371. 1987, non Willd. ex Spreng., Syst. Veg. 1: 318. 1825, nec Rottl. ex Trin., Gram. Panic. 216. 1826. I have studied all but one (*P. sylvanum*) of the types of these names, and as a result, reduce all but one (*P. lineale*) to synonymy. The synonyms I attribute to *P. fauriei* are listed under the three varieties I recognize; all the others are treated in the *Manual*. Two of the varieties need new combinations. For *P. lineale*, a species I independently recognized as new, I provide an amplified description and other additional information.

Panicum fauriei Complex

This is a distinctive coastal species characterized by an annual habit; short stature; usually branching, puberulent culms; loosely involute blades, puberulent below and velutinous above; and small panicles with appressed, puberulent, or shortly pubescent branches. Before St. John's (1987) paper, this group had in recent years been recognized as five species. I believe that three varieties are recognizable primarily on the basis of spikelet differences as summarized in the following key:

1a. Spikelets 1.5–2.3 mm long, mostly acute, sometimes acuminate, glabrous ..... var. *fauriei*
1b. Spikelets 1.8–4.2 mm long
  2a. Spikelets 2–4.2 mm long, acuminate to acute, shortly pubescent except for prominent tufts of hairs toward the tips of the glumes ..... var. *latius*
  2b. Spikelets 1.8–2.3 mm long, acute, shortly pubescent ..... var. *carteri*

Panicum fauriei A. Hitchc., Mem. Bernice Pauahi Bishop Mus. 8(3): 182, fig. 71. 1922. TYPE: U.S.A. Hawaii: [Molokai], Halawa, June 1909, *Faurie 1318* (holotype, US; isotype, BM).

The length of the glumes in plants with predominantly acuminate spikelets often varies from acuminate to shortly acuminate or acute within the same inflorescence; thus, plants assigned to var. *latius* are very variable in spikelet length. Plants that display the most strongly expressed characteristics of var. *latius* occur on Lanai and Oahu. On other islands (Kaui, Molokai, Maui, Kahoolawe, and Hawaii), as well as in other populations on Oahu and Lanai, the tufts of hairs tend to be shorter and the spikelets tend to be less acuminate and more often acute. Since stem, leaf, and inflorescence morphology are virtually identical in the complex, and since the shape of glumes is demonstrably variable within and among populations and individuals, the only reasonably useful character is glume pubescence, which ranges from absent to shortly pubescent, sometimes with increasingly prominent apical tufts of long hairs. I believe this variation is indicative of varieties.

Panicum fauriei var. **fauriei**

P. degeneri Potzal, Mitt. Bot. Gart. Mus. Berlin-Dahlem 1: 128, fig. 1. 1953. TYPE: U.S.A. Hawaii: Hawaii, N of Kaahola Light House, Hawi, in prostrate tufts on soil washed by ocean spray during storms, more resistant to salt than neighboring *Digitaria henryi*, 8 Feb. 1952, *Degener 21807* (holotype, B not seen; isotypes, K, MO, US).

P. moomomiense St. John, Rhodora 78: 543, fig. 1. 1976. TYPE: U.S.A. Hawaii: Molokai, Moomomi, limestone sand dune, 1 mi. SW of beach, 21 Jan. 1973, *Pekelo, Jr. 18* (holotype, BISH not seen).

P. sylvanum St. John, Phytologia 63: 372. 1987. TYPE: U.S.A. Hawaii: Maui, Maliko Bay, *Sylva s.n.* (BISH not seen).

The holotype of *P. degeneri* is described and illustrated as having a line of short hairs along the midnerve. Such hairs are not evident in all spikelets of the cited isotypes and when present are so sparse and small that the spikelets are essentially glabrous.

Although I have not seen the holotype of *P.*

moomomiense, I have studied the two paratypes (*Pekelo 8, 303*, both BISH) and one topotype (*Herbst & Pekelo 2948*, BISH). They represent plants with spikelets 1.8–2 mm long, which is in the lower size range for the variety, but they are in no way significantly different from the variation pattern of the variety.

I also have not seen the type of *P. sylvanum*, but the illustration and description leave no doubt that this specimen belongs to var. *fauriei* because of its glabrous spikelets 1.7–2 mm long.

Panicum fauriei var. **latius** (St. John) Davidse, stat. nov. *P. nubigenum* Kunth var. *latius* St. John, Phytologia 47: 376. 1981. TYPE: U.S.A. Hawaii: Kahoolame Island, on sea cliff of rocky coast W of Waikahalulu Bay, E of Hanakanaea Cove (Smuggler's Cove), ca. 100 ft., 21 Apr. 1980, *Cuddihy & Char 349* (holotype, BISH).

P. nubigenum sensu Hitchcock (1922), non Kunth (1833).

P. ninoleense St. John, Phytologia 63: 371. 1987. TYPE: U.S.A. Hawaii: Ninole Island, Wailua Ninole, Kan Dist., in gravel on top of basalt point, 30 ft., 25 Dec. 1949, *St. John, Hatheway & Morton 23954* (holotype, BISH).

The name *P. nubigenum* Kunth was misapplied by Hitchcock (1922) to *P. fauriei* var. *latius*. Kunth's name was a nomen novum for *P. montanum* Gaud., non Roxb. However, the type of *P. montanum* Gaud. [Insulis sandwicensibus, 1829, *Gaudichaud s.n.* (holotype, P not seen, fragment, US; isotype, K)] actually is a depauperate specimen of *P. torridum* Gaud. This is evident from the flat rather than loosely involute blades, spikelets with hairs mostly 2–2.5 mm long, borne mainly from just below the middle of the glumes to the beginning of their acuminate tips (rather than primarily at the tip), and more pilose branches.

Mature spikelets of the holotype of *P. ninoleense* are 2–2.6 mm (not 1.5–2 mm as in the description) and have the pubescence pattern of var. *latius*.

Panicum fauriei var. **carteri** (Hosaka) Davidse, comb. et stat. nov. *P. carteri* Hosaka, Occas. Pap. Bernice Pauahi Bishop Mus. 17: 67, fig. 1. 1942. TYPE: U.S.A. Hawaii: Oahu, Mokolii Islet, off coast of Oahu, rocky ledge on north end of islet, rare, 10 ft., 6 Nov. 1941, *Hosaka & Maneki 2611* (holotype, BISH not seen; isotypes, K, US).

P. annuale St. John, Phytologia 63: 368. 1987. TYPE: U.S.A. Hawaii: West Maui, Wailaku Dist., Kahakuloa, mouth of Makamukaole Stream, right side, coastal vegetation, 15 ft., 7 July 1978, *Sylva & Clarke s.n.* (holotype, BISH).

P. kukaiwaaense St. John, Phytologia 63: 370. 1987. TYPE: U.S.A. Hawaii: East Molokai, N coast, Kukaiwaa in bare dirt just above sea cliff, 29 Aug. 1984, *Hobdy 2184* (holotype, BISH).

P. malikoense St. John, Phytologia 63: 371. 1987. TYPE: U.S.A. Hawaii: Maui, ½ Haiku of Maliko Gulch, sea headland, 50–150 ft., open vegetation, 19 Dec. 1976, *Sylva s.n.* (holotype, BISH).

The types of *P. annuale*, *P. kukaiwaaense*, and *P. malikoense* are very similar, but they differ slightly in spikelet size. The lower glume is very sparsely pubescent in all three specimens, which is the reason they are assigned to var. *carteri*.

One of the practical effects of this reclassification of *P. fauriei* is that the legal status of *P. carteri* may require reevaluation since it has been legally declared as endangered (Cook, 1981; Arnett, 1983). I interpret the Mokolii Island population, *P. carteri*, sensu stricto, to represent one of several populations of var. *carteri* spread over at least two other islands (Maui, Hawaii).

Panicum lineale St. John, Phytologia 63: 370. 1987. TYPE: U.S.A. Hawaii: Kauai, ridge 1,300 ft. S of Kulanaililia, 1,400 ft., steep ledges in openings in moderately wet forest, bunchgrass 1½ ft. tall, 4 Mar. 1978, *Christensen 324* (BISH).

Densely caespitose perennial bunchgrass, 55–126 cm tall; culms erect, unbranched, glabrous. Leaves primarily basal, often strongly distichous; sheaths glabrous or puberulent toward the apex; ligule a rudimentary membrane with cilia 0.4–0.6 mm long; collar densely velvety puberulent, especially on the sides; blades 59–85 cm long, 4–9 mm wide when unrolled but mostly involute, glabrous below, densely velvety pubescent above at the base behind the ligule and the lower portion, otherwise glabrous, the tip long-acuminate. Panicles 20–35 cm long, 6–10 cm wide; rachis glabrous; branches spreading at acute angles, very sparsely scaberulous, the pulvini pubescent. Spikelets 3.8–4.8 mm long, linear-lanceolate, acuminate, glabrous; rachillar internodes prominent; glumes unequal, the lower 1.7–2.6 mm long, 3–7-nerved, acute, the upper 3.4–4.5 mm long, 9-nerved, acuminate; lower floret sterile; lower lemma as long as the spikelet, similar to the upper glume, 7–9-nerved; lower palea $\frac{1}{5}$–$\frac{2}{3}$ as long as the lower lemma, narrow, acuminate; upper floret 2.5–2.9 mm long, 0.7–0.8 mm wide, linear-elliptic, cartilaginous, smooth, shiny, acute, the lemma and palea equal in length; anthers 3, 1.7–2.4 mm

long, orange; styles 2, separate; stigmas plumose, purple; caryopsis 1.6–1.7 mm long, 0.7 mm wide, oblong-elliptic, the embryo 0.8 mm long, the hilum 0.4–0.5 mm long, basal, elliptic.

Additional specimens examined. U.S.A. HAWAII: Kauai, Kalahu, W rim of Kalalau Valley, precipitous slope at 3,000 ft., single specimen seen, 1 Feb. 1950, *Degener & Hatheway 20444* (US); Kauai, Na Pali Coast, between Waiahuakua and Hoolulu Valley, ca. 600 ft., large bunchgrass growing beside trail with *Eragrostis variabilis*, 10 Apr. 1980, *Corn ESP 190* (BISH); Kauai, along a steep, wet ridge running up the W slope of Wainiha Valley to SW of Kulanaililia, forest of *Metrosideros*, *Eugenia*, etc., bunchgrass, anthers conspicuously orange, quite common, 400 m, 20 Mar. 1976, *Fay, Moriarity & Robinson 588* (BISH, K, MO, PRE, SI, US).

Panicum lineale is so far known only from the moist, northwestern windward side of Kauai. Although it is a prominent grass, it must be very localized, judging from the paucity of collections. J.J. Fay (pers. comm.) collected this species at the margin of a pasture. Fay also noted that clumps of this grass pulled out of the ground readily, and this may indicate that it does not persist long in secondary areas that are subject to grazing.

This species is amply distinct from all other native *Panicum* (s. str.) species by its short lower glume and long, narrow spikelets. All others have a lower glume as long as or slightly shorter than the spikelet.

Although this species probably belongs to subg. *Panicum* sect. *Panicum* (sensu Hsu, 1965), a good understanding of its precise relationships eludes me. Anatomical studies of its leaves, lemmas, and lodicules would probably make such a determination easier.

Specimens of the *Fay et al. 588* collection have been distributed with the unpublished name *P. napaliensis*.

I thank John J. Fay, U.S. Fish and Wildlife Service, Endangered Species Office, for access to his excellent collections and for observations about *P. lineale*.

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THREE NEW SPECIES OF FERNS FROM MESOAMERICA

The following new species are described as part of my work on the pteridophyte volume for *Flora Mesoamericana*.

Tectaria acerifolia R. C. Moran, sp. nov. TYPE: Panama. Panamá: El Llano to Cartí road, 200 m, *Churchill & de Nevers 4200* (holotype, MO; isotypes, PMA, UC). Figure 1a, b.

Petiolus castaneus, laminam fere aequans. Lamina palmatiloba; soris seriebus 3–8 inter venas principales dispositis; indusiis reniformibus vel circularibus, haud peltatis.

Rhizome erect; sterile and fertile leaves dimorphic; petiole of sterile leaves ca. equaling the lamina, castaneous throughout, puberulent, scaly at base, the scales 1–2 mm long, 0.2–0.5 mm wide, lanceolate, spreading; lamina 14–29 cm long, palmately lobed; basal lobes or pinnae 12–18 cm long, falcate, entire but with 1–2 short basal basiscopic lobes; rachis and costae castaneous towards the base, tan distally, sparsely puberulent, the hairs ca. 0.1 mm long, inconspicuous; laminar tissue glabrous on both surfaces, drying dull green; petioles of the fertile leaves 2–3 times longer than the lamina; the fertile laminae 15–20 cm long; sori in 3–8 rows between the principal veins; indusia nonpeltate, attached laterally, reniform or circular.

Additional specimens examined. COSTA RICA. ALAJUELA. Upala, Bijagua El Pilón, de la intersección del camino San Miguel a El Pilón con el Río Chimurria, 600 m, *Herrera 2061* (MO). PANAMA. CANAL ZONE: Parque Nacional Soberanía, camino del Oleoducto, *Vasquez 239* (MO). COLÓN: 9–12 mi. E of Trans-Isthmian Hwy. on Santa Rita Ridge, 500–550 m, *Thompson 4850* (CM, MO). PANAMÁ: Cerro Jefe, 6 mi. past Cerro Azul on road to Altos Pacora, 800 m, *Sytsma & D'Arcy 3680* (MO); 5–9 mi. N of Pan-American Hwy. on El Llano–Carti road, 200–250 m, *Thompson 4631* (CM). SAN BLAS: forest SE of Puerto Obaldia, *Croat 16842* (MO).

This species grows in wet forests at 200–800 m. It can be distinguished from all other tectarias in the New World by the combination of palmately divided leaves, dark axes, sori in 3–8 rows between the lateral veins, and fertile leaves with longer and more erect petioles than those of the sterile ones. It resembles *T. heracleifolia*, a species which differs by its peltate indusia, sori in 2–3 rows between the principal veins, stramineous axes, and usually 1-pinnate leaves.

Bolbitis simplex R. C. Moran, sp. nov. TYPE: Panama. Darién: Parque Nacional del Darién, ridge between N & S branches of Río Pucuro, in forest N of old village of Tacarcuna, ca. 18 km E of Pucuro, terrestrial on slopes along small stream, 600–800 m, *Hammel et al. 16467* (holotype, MO; isotypes, F, PMA, UC, US). Figure 1c, d.

Folia simplicia, integra, anguste oblanceolata ad anguste elliptica, apice gemma prolifera munita; venis areolas venulis inclusis formantibus; rhachidi dimidio proximali abaxialiter anguste alata.

Terrestrial; rhizome 4–6 mm wide, short-creeping, horizontal, scaly, the scales 2–4 × 0.5–1 mm, blackish, opaque; sterile and fertile leaves dimorphic; sterile lamina 23–50 cm long, 3.5–5 cm wide, simple, entire, narrowly oblanceolate to narrowly elliptic, cuneate, glabrous, with a subterminal bud; petiole 1–5 cm long, alate, scaly, the scales lanceolate, brown, spreading, nonclathrate; rachis with a narrow abaxial wing ca. 0.5 mm wide, best developed in the proximal half, parallel (not perpendicular) to the lamina; veins anastomosing, the areoles with recurrent free veinlets; fertile leaves 30–50 cm long, 0.7–1.1 cm wide, long-petiolate.

This new species resembles *Bolbitis pandurifolia* (Hook.) C. Chr. because both have simple leaves, subterminal buds, and areoles with included veinlets. The two species differ in several obvious characteristics of the sterile leaves. The petioles on sterile fronds of *B. simplex* are 1–5 cm long (about $\frac{1}{10}$ the length of the lamina), whereas those of *B. pandurifolia* are 16–27 cm long (about ½ the length of the lamina). The sterile lamina of *B. simplex* is 3.5–5 cm wide, narrowly oblanceolate to narrowly elliptic, and cuneate basally, whereas that of *B. pandurifolia* is 6–12 cm wide, elliptic, oblong, or ternate with a single pair of basal pinnae, and short-decurrent, subcordate, or auriculate basally. The rachis of *B. simplex* has an abaxial, green, herbaceous wing, whereas that of *B. pandurifolia* lacks such a wing. Aside from morphology, the geography also differs: *B. simplex* is known from eastern Panama, whereas *B. pandurifolia* is known from central Ecuador to central Peru.

Salpichlaena thalassica Grayum & R. C. Moran, sp. nov. TYPE: Costa Rica. Heredia: forest

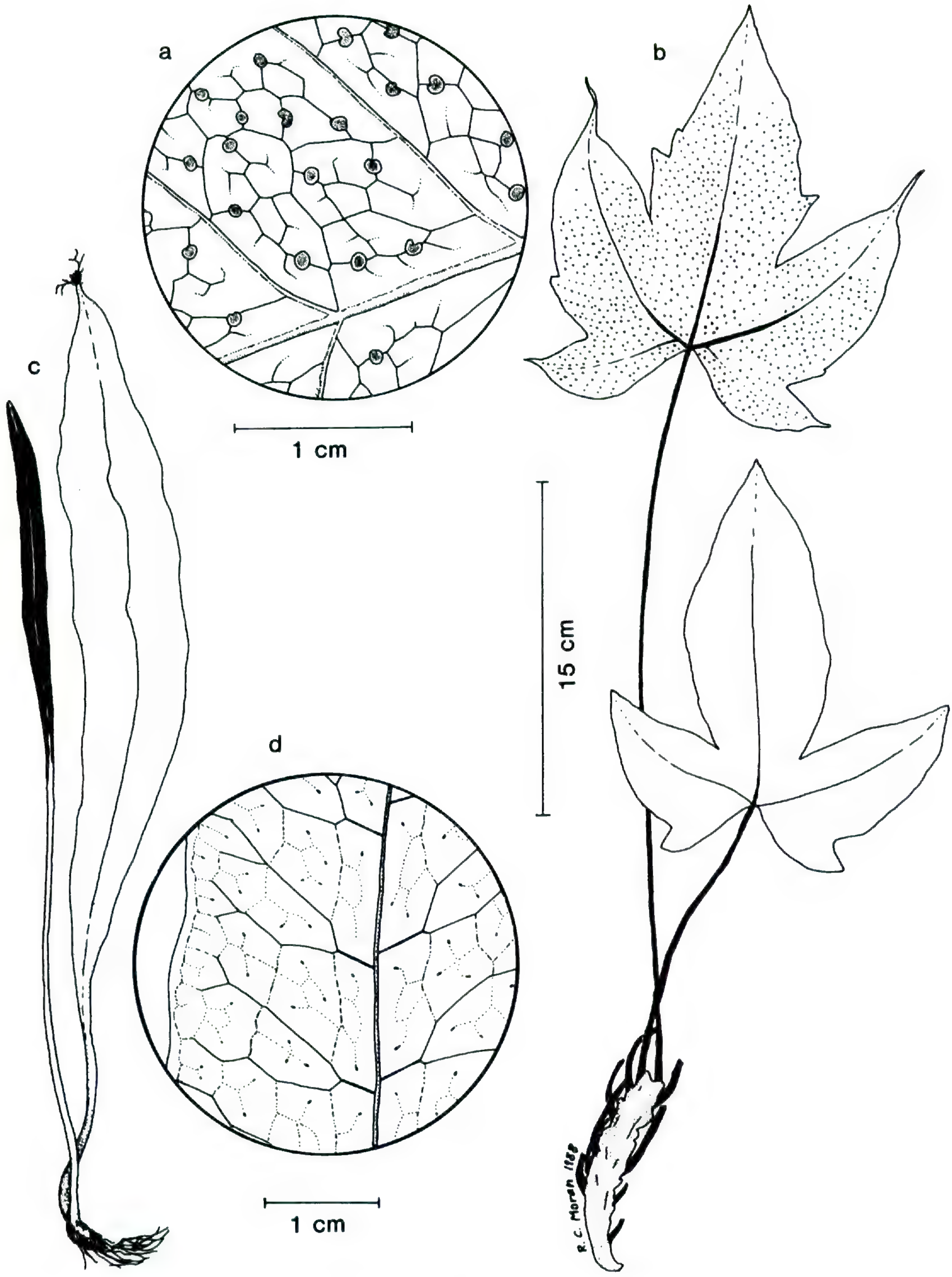

FIGURE 1. a, b. *Tectaria acerifolia* (*Vásquez 239* MO).—a. Abaxial surface of fertile leaf.—b. Sterile and fertile leaves, note longer petiole of the fertile leaf.—c, d. *Bolbitis simplex* (*Hammel et al. 16467* MO).—c. Sterile and fertile leaves.—d. Adaxial surface of the sterile leaf.

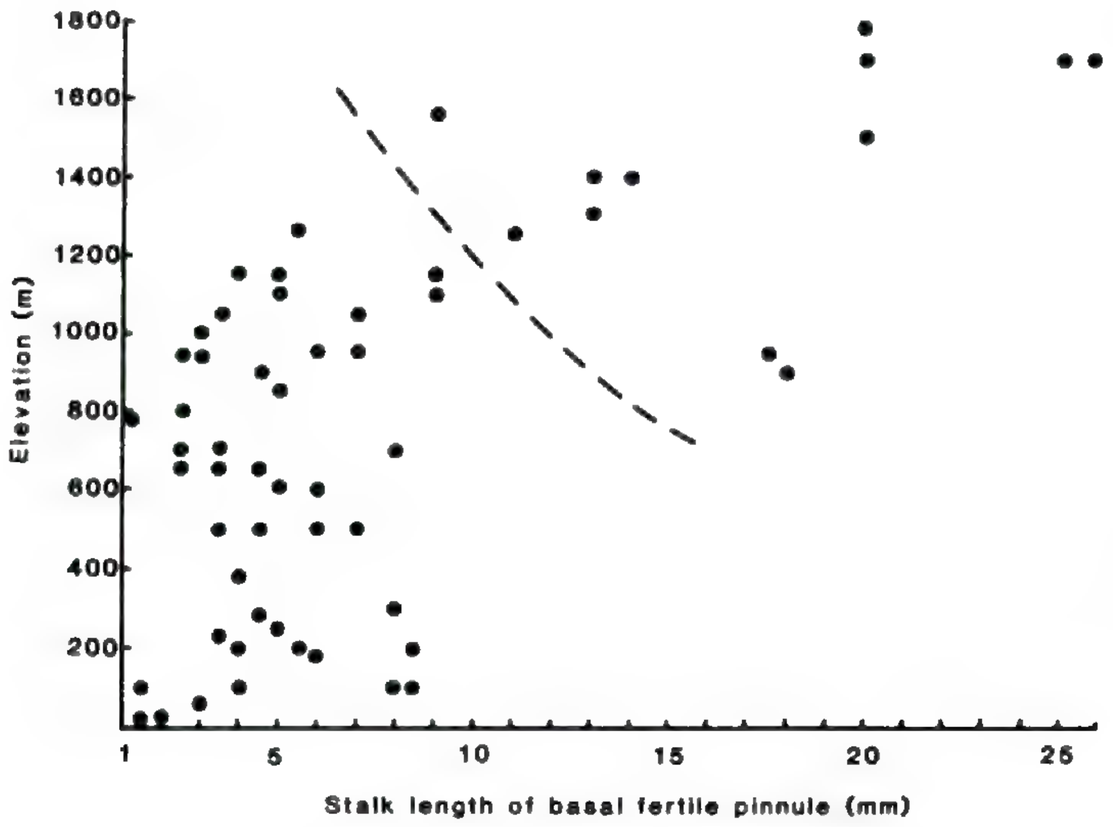

FIGURE 2. Elevation versus stalk length of the basal fertile pinnule in *Salpichlaena thalassica* (upper right; leaves blue-green) and *S. volubilis* (lower left; leaves dark green). Specimens measured were from Costa Rica and Panama.

between Río Peje and Río Sardinalito, Atlantic slope of Volcán Barva, 10°17′N, 84°4.5′W, 800–1,000 m, *Grayum & Chazdon 6833* (holotype, MO; isotype, CR).

Species haec ab *S. volubili* differt stipite longiore (9–26 mm) pinnulae basalis fertilis, foliis thalassicis, distributione altitudinali superiore.

Additional specimens examined. NICARAGUA. ZELAYA: Cerro La Pimienta, bosque enano, 1,000–1,200 m, *Grijalva 346* (CR); costado SW de Cerro El Hormiguero, 900–1,000 m, *Grijalva 470* (CR), *489* (CR); Cerro El Hormiguero, dense, virgin elfin forest, 1,100–1,183 m, *Pipoly 5187* (MO). COSTA RICA. CARTAGO: El Muñeco, S of Cartago, 1,350 m, *Stork 2711* (UC); Tapantí, Quebrada Segunda, *Berrocal & Sánchez 122* (CR), *123* (CR); Tapantí, 1,700 m, *Berrocal & Sánchez 122* (CR), *123* (CR); ca. 15 km S of Tapantí along the new road, on the E slope of the Río Grande de Orosi near the concrete bridge, 1,500 m, *Burger & Liesner 6807* (MO, NY, UC); mountains ca. 5 mi. S of Cartago, *Maxon 512* (NY). HEREDIA: Braulio Carillo National Park, 1,215 m, *Hennipman et al. 6893* (MO). PUNTARENAS: Monteverde, Veracruz River Valley S of reserve, 1,300–1,500 m, *Haber ex Bello & Clagett 5383* (MO). PANAMA. CHIRIQUÍ: trail W from Fortuna Dam Camp to La Fortuna, broad-leaved cloud forest, 1,300 m, *Hampshire & Whitefoord 370* (BM). DARIÉN: Mamey, ridge, 450 m, *Whiteford & Eddy 357* (CR); Cerro Mali base camp, Colombian border, 1,400 m, *Gentry & Mori 13754* (CR, MO). COLOMBIA. ANTIOQUIA: Mpio. Fontino, road to Murrí, 15 km W of Nutibara (Altos de Cueva), 1,850 m, *Brant & Martínez 1386* (MO, UC). BOYACÁ: carretera Chinquinquirá a Pauna, 1,900 m, *Jaramillo et al. 3541* (MO). MAGDALENA: Sierra Nevada de Santa Marta, Cerro Ratón, Serranía de San Javier, 1,900 m, *Forero & Kirkbride 672* (MO). META: Sierra de la Macarena, Central Mts., N ridge, 1,500 m, *Philipson & Idrobo 1838* (BM). NARIÑO: Ricáurte, 1,300 m, *von Sneidern A.603* (MO); Reserva Natural La Planada, a 7 km de Chuncunés, 1,800 m, *de Benavides 9013* (MO).

This species was first noted by Dr. Michael Grayum, who observed that the leaves were blue-green rather than dark green, as in *S. volubilis*. His extensive fieldwork in Costa Rica has shown that the blue-green-leaved plants generally grow at higher elevations than *S. volubilis*, an observation supported by elevational data on herbarium specimens (Fig. 2). Further study of herbarium specimens found a quantitative character: the length of the stalk of the basal fertile pinnule was longer in the blue-green-leaved plant than in *S. volubilis* (Fig. 2). The lengths of the spores and characteristics of the stem scales were also checked, but these showed no differences with those of *S. volubilis*.

It was decided to recognize as a new species the plants with blue-green leaves because elevation and length of the basal fertile pinnule stalk correlated well, overlapping only slightly with those features of *S. volubilis*. Because of the overlap, it could be argued that *S. thalassica* is best treated as a subspecies or variety; however, Michael Grayum and I decided to treat it as a species to bring it to the forefront of pteridologists' attention.

I first noted that these species were undescribed while I was a National Science Foundation postdoctoral fellow for the *Flora Mesoamericana* project (BSR-8614880). I thank John Dwyer and Roy Gereau for checking the Latin descriptions.

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TWO NEW SPECIES OF *ELAPHOGLOSSUM* (ELAPHOGLOSSACEAE) FROM AMAZONAS, VENEZUELA

Elaphoglossum is one of the most complex and taxonomically difficult of all fern genera with over 600 species, three-fourths of which occur in the New World. Ninety-nine species were treated in Smith's *Pteridophytes of Venezuela* (1985). Twenty-nine of those species were described as new (Mickel, 1987), and I here describe two additional species.

Elaphoglossum longicaudatum Mickel, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, 1–2 km E and SE of San Carlos de Río Negro, 01°51′N, 67°03′W, 11 Nov. 1987, *Liesner & Carnevali 22993* (holotype, NY; isotypes, MO, VEN). Figure 1A–C.

Ab *E. auricomo* rhizomatis paleis atrorubrobruneis laminaque apice caudata divergens.

Rhizome compact, 3–6 mm diam.; rhizome scales linear-lanceolate, lustrous, heavily indurated, dark red-brown, 2–3 mm long, margin with sparse, weak, hairlike teeth, apex twisted; phyllopodia inconspicuous; fronds clumped, 12–32 cm long, 1.9–3.4 cm broad; stipe 1–3 cm long, 1/30–1/8 the sterile frond length, densely clothed with spreading orange scales 3–5 mm long; blade narrowly oblanceolate, papyraceous, apex caudate, base narrowly cuneate; veins indistinct, free, simple or 1-forked, ca. 1 mm apart, at 75° angle to costa; hydathodes lacking; blade scales orange, dense but not strongly overlapping, linear-lanceolate, 1–2 mm long, mostly skeletonized with long hairlike teeth, the teeth twice as long as the width of the scale body, some scales reduced nearly to stellate hairs; fertile fronds ca. ½ the sterile frond length, 11 cm long; stipe 3 cm long; blade linear, 8 cm long, 0.7 cm broad, apex cuspidate, base cuneate, densely imbricate-scaly above, costa densely scaly below; intersporangial scales lacking.

Epiphytic in "transitional forest between bana and taller forest" (type specimen), 120 m elevation.

Additional specimen examined. VENEZUELA. AMAZONAS: 2 km E and SE of San Carlos de Río Negro, 01°51′N, 67°03′W, 12 Nov. 1987, *Liesner & Carnevali 23003* (NY).

Elaphoglossum longicaudatum differs from *E. auricomum* (Kunze) Moore in having dark (rather than pale) rhizome scales and caudate (rather than acuminate) blade apex.

Elaphoglossum parvulum Mickel, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Atures, forested area along stream, on plateau N of unnamed (1,760 m) peak, 9 km NW of settlement of Yutajé, 4 km W of Río Coro-Coro, W of Serranía de Yutajé, 05°41′N, 66°10′W, 7 Mar. 1987, *Liesner & Holst 21772* (holotype, NY; isotypes, MO, VEN). Figure 1D–F.

Elaphoglosso horridulo similis laminae forma hydathodisque conspicuis sed pilis multis glandulosis differt.

Rhizome compact, ascending, ca. 2 mm diam.; rhizome scales linear, orange, entire, 2–3 mm long; phyllopodia lacking; fronds clumped, 2–5 cm long, 0.5–0.7 cm broad; stipe slender, 1/4–3/5 the sterile frond length, clothed with spreading, orange, hairlike, subulate scales ca. 2 mm long and with abundant 3–5-celled erect glandular hairs; blade linear-oblong, papyraceous, apex obtuse, base narrowly cuneate; veins obscure; hydathodes present and conspicuous; blade scales hairlike, subulate, denticulate, castaneous, 2–3 mm long, with abundant erect glandular hairs; fertile fronds ca. as long as the sterile fronds; stipe ca. 1/5 the fertile frond length; blade smaller than on the sterile fronds, spatulate; intersporangial scales lacking.

Epiphytic, 1,050–1,300 m elevation.

Elaphoglossum parvulum resembles *E. horridulum* (Kaulf.) J. Smith in blade shape and conspicuous hydathodes but has many glandular hairs. It is probably more closely allied to *E. siliquoides* (Jenm.) C. Chr. but is much smaller than that species (fronds 2–5 cm long vs. 17–50 cm).

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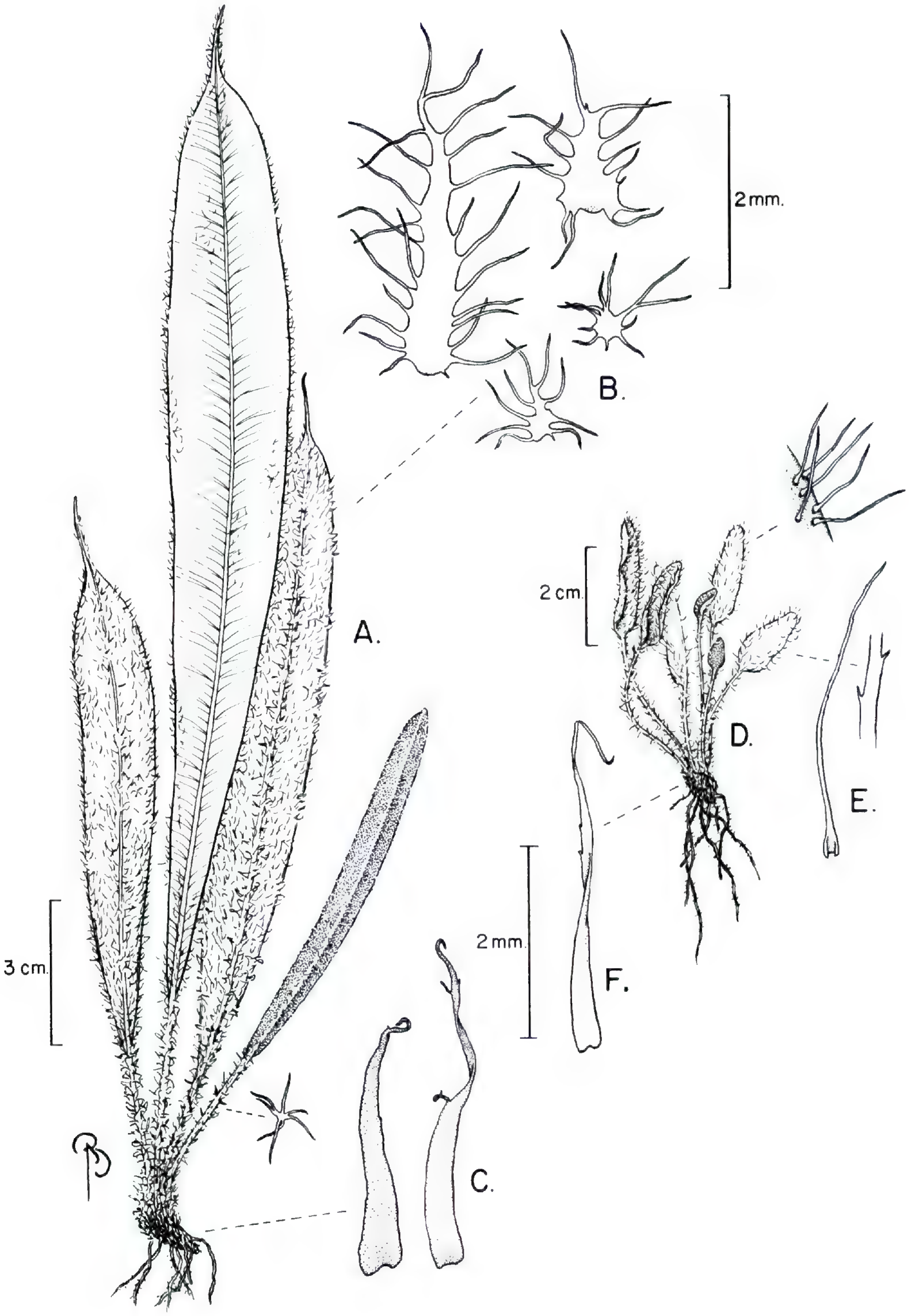

FIGURE 1. A–C. *Elaphoglossum longicaudatum.*—A. Habit.—B. Rhizome scales.—C. Blade scales. D–F. *Elaphoglossum parvulum.*—D. Habit.—E. Blade scales.—F. Rhizome scales.

A NEW COMBINATION IN *LUDWIGIA* (ONAGRACEAE)

Jussiaea dodecandra has been described by De Candolle (1828) based on material collected in Guyana. This taxon has been considered as a variety of *Jussiaea affinis* DC. (Munz, 1942) or *Ludwigia affinis* (DC.) Hara (Munz, 1965) of sect. *Seminuda*, based on its minutely puberulent pubescence, which differs from the pilose indument of *Ludwigia affinis*. Recent relevant differential data indicates that the chromosome number for this taxon is $n = 24$ (this paper). This is different from *Ludwigia affinis* with $n = 32$ and 40 (Raven & Tai, 1979) and has so far been reported in this section for two other unrelated species (Raven & Tai, 1979; see also key below). As a result, we consider this taxon to be best treated at the specific level, for which the new combination is needed.

Ludwigia dodecandra (DC.) Zardini & Raven, comb. nov. *Jussiaea dodecandra* DC. Prodromus 3: 53. 1828. *Jussiaea affinis* var. *dodecandra* (DC.) Munz, Darwiniana 4: 261. 1942. *Ludwigia affinis* var. *dodecandra* (DC.) Munz, N. Amer. Fl., ser. 2, 5: 36. 1965. TYPE: Guyana. Demerara, *Parker in 1826* (holotype, G-DC, photos POM and F 7897; isotypes, K, U).

Voucher for chromosome number, $n = 24$, counted by Hongya Gu: French Guiana. Saül, entrée du village, *Granville et al. 9062* (CAY, MO).

Additional specimens examined. COSTA RICA. GUANACASTE: El Arenal, *Standley & Valerio 45417* (F). PANAMA. BOCAS DEL TORO: Chiriquí Lagoon, *Wedel 1884* (MO); Changuinola River, *Dunlap 391* (F). CANAL ZONE: Barro Colorado Island, north shoreline of Gigante Bay, *Croat 13972* (MO). COCLÉ: boca del Toabré, confluence Río Toabré and Río Coclé del Norte, *Lewis et al. 5564* (MO). COLÓN: ca. 0.5 km from Río Buenaventura, near Portobelo, *Kennedy 2238* (MO). COLOMBIA. CHOCÓ: Acandí, *Ordoñez et al. 072* (MO). FRENCH GUIANA: St. Laurent-Paul Isnard, between PK 100 and 120, *Granville 5198* (CAY, MO); *Granville 5197* (CAY, MO); Montagne Bellevue de l'Inini, *Granville et al. 8074* (MO), *7852* (MO); Saul, tracé ORSTOM Belvedere Est PK 2, *Granville 3137* (CAY, MO); Saul, Carbet Mais Trail, vicinity of Crique Popote, *Prance 28108* (MO); River Approuage, between "saut" and crique Couata, *Oldeman T-61* (CAY, MO); region of contact between Sommet Tabulaire and Massif des Emerillons, *Granville 3747* (CAY, MO); Monts Bakra, 3 km W of Pic Coudreau, *Granville 4138* (CAY, MO). GUYANA: Mbura Hill, *Maas et al. 5899* (MO).

Ludwigia dodecandra can be distinguished from the other species of sect. *Seminuda* by the following key:

KEY TO DISTINGUISH THE SPECIES OF *LUDWIGIA* SECT. *SEMINUDA*

1a. Flowers 4-merous.
  2a. Sepals 2.5–4.5 mm long, plants finely puberulent, $n = 24$ ..... *Ludwigia africana* (Brenan) Hara
  2b. Sepals 6–10 mm long, plants pilose, $n = 8$ ..... *Ludwigia quadrangularis* (Mich.) Hara
1b. Flowers 5–6-merous.
  3a. Leaves lanceolate, sepals 5–8 mm long, disc flat, raphe 1/6–1/8 the width of the seed body, $n = 16, 24$ ..... *Ludwigia leptocarpa* (Nutt.) Hara
  3b. Leaves ovate, sepals 3.5–5 mm long, disc elevated, raphe 1/3–1/4 the width of the seed body.
    4a. Plants pilose, $n = 32, 40$ ..... *Ludwigia affinis* (DC.) Hara
    4b. Plants minutely puberulent, $n = 24$ ..... *Ludwigia dodecandra* (DC.) Zardini & Raven

We are grateful to Jean-Jacques de Granville for providing materials for chromosome counts and to Hongya Gu for counting them.

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PSYCHOTRIA BERRYI, A NEW NAME FOR *P. DAVIDSAE*

Steyermark named *Psychotria* "*davidsae*" after his co-collector (Davidse, male) of the type specimen, not noticing that the *International Code of Botanical Nomenclature*, Art. 73.10, stipulates that the epithet must be corrected to davids*ei*, which makes the name an illegitimate homonym. As all three collectors of the type specimen already have *Psychotria* species named after them, I rename the species as follows, after the first-named co-collector of a paratype.

Psychotria berryi Wingfield, nom. nov. based on *P. davidsei* Steyerm. (as "*davidsae*"), Ann. Missouri Bot. Gard. 71: 1177. 1985, non *P. davidsei* Dwyer, Ann. Missouri Bot. Gard. 67: 368. 1980.

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Ann. Missouri Bot. Gard. 77: 597. 1990.

NEW SPECIES OF *GUATTERIA* (ANNONACEAE) FROM THE GUAYANA HIGHLAND

In preparing the treatment of *Guatteria* Ruiz & Pavón for the *Flora of the Venezuelan Guayana* by J. A. Steyermark and collaborators, we found two species from the *Flora* region to be apparently undescribed. Formal descriptions for these taxa, *Guatteria liesneri* and *G. atabapensis*, are provided below. An additional species from nearby Guyana, *G. clusiifolia*, is described as well.

Guatteria liesneri D. M. Johnson & N. A. Murray, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, along Río Baria (= Río Mawarinuma) just upstream from base camp, SW side of Cerro de la Neblina, 140 m, 15 Feb. 1985 (fl, fr), *Nee 30864-a* (holotype, NY; isotypes to be distributed).

Species forsan *Guatteriae modestae* Diels proxima et ramulis glabris, foliis nitidis glabris conspicue reticulatis, et venis secundariis divaricatis similis, sed lamina foliorum 14.6–22.1 cm longa et 5.1–7.0 cm lata oblonga vel oblongo-elliptica et monocarpiis 9–10 mm longis et 4–5 mm latis stipite 15–20 mm longo sustentis diversa.

Tree 4–20 m tall with a DBH of 10 cm in one individual. Twigs glabrate. Laminas of larger leaves 14.6–22.1 cm longa et 5.1–7.0 cm lata oblonga vel ceous, oblong or oblong-elliptic; base broadly cuneate to rounded, short-decurrent; apex cuspidate or short-acuminate, the acumen 13–20 mm long; glabrate or with sparse minute hairs abaxially; midrib plane or slightly impressed adaxially, raised abaxially; secondary veins 15–19 per side, diverging at 60–75° to midrib, brochidodromous, closing 3.5–8.5 mm from the margin, raised on both surfaces of the blade; higher-order veins raised and conspicuous on both surfaces of the blade. Petiole 8–13 mm long, 1.5–2.2 mm wide, winged, involute toward base, glabrate. Pedicels 1–2 per leaf axil, occasionally from axils of fallen leaves, 1.2–2.7 cm long, 0.7–1.2 mm wide, articulate 2–7 mm above the base, with minute caducous bracteoles below articulation, glabrate. Sepals 3–4 mm long, 2.5–3 mm wide, free and contiguous at base, chartaceous, triangular to ovate, acuminate at apex, sericeous abaxially, sparsely sericeous or glabrate adaxially. Largest petals 14–19 mm long, 8–10 mm wide, subcoriaceous, oblong, elliptic, or widest above middle, adaxially pubescent with the hairs densest at base, abaxially pubescent with a glabrous patch at base on inner petals. Stamens ca. 1.4 mm long, oblong, connectives truncate at the apex, papillate. Carpels ca. 100–120; ovaries sericeous, ca. 0.7 mm long; styles coherent, ca. 1.2 mm long, clavate, pubescent on sides, more densely so at apex. Torus 4–5 mm diam., with a rim between stamens and carpels, glabrate. Pedicel in fruit 1.8–2.1 cm long, ca. 1.5 mm thick, articulate 3–5 cm above base, glabrate, with a few small lenticels; torus in fruit depressed-globose, expanded or not, sparsely pubescent. Monocarps up to 60, the seed-containing portion 9–10 mm long, 4–5 mm wide, ellipsoid, apiculate at apex, stipe 15–20 mm long, 0.7–1.0 mm wide, glabrate or with a few sparse hairs, pericarp 0.1 mm thick. Seed 8 mm long, 5 mm wide, ellipsoid, orange-brown, smooth, shiny, the exostome paler than seed coat, slightly exserted.

Additional specimens examined. BRAZIL. AMAZONAS: Rio Negro, Jucabi (near mouth of Rio Curicuriari) and vicinity, 21–25 Sep. 1947, *Schultes & Lopez 8856* (NY). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Atabapo, road from San Fernando de Atabapo to Santa Barbara, 12–40 km from San Fernando, 24 Mar. 1974 (MO, NY); Dept. Río Negro, from Los Tambores of Comisión de Limite to Caño Erubichi on Río Baria, 2 Apr. 1984 (fl), *Liesner 17120* (MO, NY); Dept. Atures, road Pte. Cataniapo–Gavilán, 20–25 km SE of Puerto Ayacucho, 4 Nov. 1980 (fl), *Maas & Huber 5106* (VEN). DEPT. RÍO NEGRO: Neblina Base Camp on the Río Mawarinuma, 17 July 1984 (bud), *Davidse & Miller 27447* (MO); Cerro Neblina, between base camp and "Puerto Chimo" along Río Mawarinuma, 26 Apr. 1984 (fl), *Gentry & Stein 46949* (MO, NY), *46983* (MO, NY); 1 to 4 km E of Cerro de La Neblina Base Camp on Río Mawarinuma, 10 Feb. 1984 (fl), *Liesner & Funk 15287* (MO, NY); along Río Baria (= Río Mawarinuma) just upstream from base camp, SW side of Cerro de la Neblina, 27 Jan. 1985 (fl, fr), *Nee 30576* (NY, undistributed duplicates); 16 km NE of San Carlos de Río Negro on road to Solano at Caño de Cholo, 7 Apr. 1984 (fl), *Stein et al. 1472* (MO).

This species is named for Ron Liesner, in recognition of the many excellent collections of *Guatteria* that he has made in the Venezuelan Guayana, which have often helped clarify confused taxonomy. This species is placed in sect. *Pteropus* R. E. Fries by virtue of its leaves decurrent at the base

and tendency of the flowers to occur in fascicles. It resembles most closely *Guatteria modesta* Diels, described from Peru, in the glabrous shoots, the thin leaves with raised secondary and higher-order veins, and the wide-spreading secondary veins, but differs in its oblong to oblong-elliptic leaf blades 14.6–22.1 cm long and 5.1–7.0 cm wide and the monocarps with the seed-containing portion 9–10 mm long and 4–5 mm wide on stipes 15–20 mm long. *Guatteria modesta*, in contrast, has lanceolate leaf blades 10–16 cm long and 3.5–5 cm wide, and monocarps with the seed-containing portion 15 mm long and 8 mm wide on stipes 12–16 mm long. The character of the flowers is very similar, and additional collecting may prove them to be conspecific.

Guatteria atabapensis Aristeguieta ex D. M. Johnson & N. A. Murray, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Atabapo, Río Atabapo, at margin of Sabana Cumare on right bank of Caño Cumare (20 km above San Fernando de Atabapo), 125–140 m, 3 June 1959 (fl, fr), *Wurdack & Adderley 42759* (holotype, NY; isotype, F).

Species foliis coriaceis ad basim rotundatis et monocarpiis parvis brevistipitatis *Guatteriae maguirei* R. E. Fries similis, sed lamina foliorum 9.8–15.9 cm longa et 4.5–5.2 cm lata ad apicem acuminata, pedicello brevi, 0.4–0.8 cm longo, et connectivo antherarum papillato absimilis.

Treelet or shrub 3–6 m tall. Twigs pubescent, at length glabrate. Laminas of larger leaves 9.8–15.9 cm long and 4.5–5.2 cm wide, subcoriaceous to coriaceous, lanceolate to ovate, occasionally oblong; base rounded; apex acuminate, the acumen 9–15 mm long; glabrate adaxially, densely pubescent but soon sparsely pubescent to glabrate abaxially; midrib slightly impressed adaxially, raised abaxially; secondary veins 11–14 per side, diverging at 60–90° to midrib, brochidodromous, loops closing at 5–7 mm from the margin; secondary and higher-order veins raised on both surfaces of the blade, more strongly so abaxially. Petiole 5–11 mm long, 1.7–2.5 mm wide, canaliculate, glabrate. Pedicels 1–2 per leaf axil, occasionally from axils of fallen leaves, 0.4–0.8 cm long, 1–1.5 mm wide, articulate 2–3 mm above the base, pubescent, sometimes with tiny persistent amplexicaul bracteoles below articulation. Sepals 3.5 mm long, 2.5–3.5 mm wide, free or connate at base, subcoriaceous, ovate, acuminate to obtuse at apex, appressed-pubescent abaxially, sparsely so or glabrate adaxially. Outer petals 13–16 mm long, 5–5.5 (–9) mm wide, subcoriaceous, oblong or oblanceolate, rounded at apex, adaxially pubescent, hairs densest at base, abaxially pubescent, with a glabrous patch at base; inner petals 14–21 mm long, 8–12 mm wide, oblong or obovate, rounded at apex, pubescence as in outer petals. Stamens 1–1.2 mm long, long-trapezoidal, connectives truncate at the apex, papillate. Carpels ca. 40; ovaries (immature) ca. 1.1 mm long, sericeous; styles (immature) 0.8 mm long, clavate, pubescent. Torus hemispheric, 3.5–4 mm diam., with rim present between stamens and carpels, glabrate. Pedicel in fruit 0.7–0.8 cm long, ca. 1.8 mm thick, articulate above base, glabrate; torus in fruit depressed-globose or unexpanded, glabrate. Monocarps up to ca. 15, the seed-containing portion 7–9 mm long, 4–5 mm wide, ellipsoid to pyriform, apiculate at apex, stipe 4–5 mm long, 0.5–0.7 mm wide, glabrate or with a few sparse hairs, pericarp 0.2–0.3 mm thick. Seed 7–9 mm long, 4–4.5 mm wide, ellipsoid-fusiform, dark brown, sulcate and somewhat pitted, shiny, the exostome oblique, paler than seed coat.

Additional specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Atabapo, white sand savannas on the northern bank of Caño Caname, nearly opposite Cucurital de Caname, 2 May 1979 (fl, fr), *Davidse et al. 17066* (MO); Dept. Atabapo, Caño Caname, sabanas de Cucurital, Apr.–May 1979 (bud, fr), *Huber et al. 3729* (VEN); Dept. Atabapo, sabana abierta a unos 20 km al S del medio Caño Caname, 10 Mar. 1980, *Huber 5146* (VEN); Dept. Atures, sabana ubicada en la ribera izquierda (S) del Río Guayapo medio, 27 July 1980 (fr), *Huber & Tillett 5509* (VEN).

This taxon was twice proposed as new, but, as far as is known, neither Fries nor Aristeguieta ever published a description. The species appears to be confined to savannas in the immediate vicinity of San Fernando de Atabapo, where it is found in shrub islands, sometimes on white sand, at 95–100 m. It is readily distinguished from *G. maguirei*, which is sympatric in similar habits, by the shorter pedicel, papillate anther connectives, and larger leaves. It may also be confused with large-leaved forms of *G. schomburgkiana* C. Martius, which differs by having setulose anther connectives, and monocarps with the seed-containing portion 7–10 mm long and 5–7 mm wide on stipes that occasionally reach 5 mm long (more commonly 0.5–2 mm long).

Guatteria clusiifolia D. M. Johnson & N. A. Murray, sp. nov. TYPE: Guyana. Upper Mazaruni River Basin, Mt. Ayanganna, NE side of mountain, 800–900 m, 2 Aug. 1980 (fl), *Tillett, Tillett & Boyan 45009* (holotype, NY).

Inter species *Guatteriae* sectionis *Mecocarpi* forsan *G. durae* R. E. Fries arctissime similis, sed ab ea foliis glabratis ad apicem truncatis et emarginatis vel brevicuspidatis (3 mm), petalis 0.6–0.9 mm crassis, et monocarpiis 22–27 mm longis et 13–14 mm latis stipite 4 mm longis sustentis divergens.

Tree 25–35 m tall, diam. 40–80 cm at base. Twigs initially with tightly appressed pubescence, then glabrate. Lamina of larger leaves 12–15 cm long, 6.8–7.7 cm wide, subcoriaceous to coriaceous, obovate; base cuneate and decurrent; apex truncate, emarginate or short-cuspidate, the cusp to 3 mm long; surface even, initially with tightly appressed pubescence abaxially, becoming sparsely pubescent to glabrate; midrib impressed adaxially, raised abaxially; secondary veins 13–17 per side, diverging at 60–70° to midrib, brochidodromous, loops closing at 3–4 mm from the margin; secondary veins plane, slightly raised or slightly impressed adaxially, raised abaxially; higher-order veins indistinct. Petiole 14–20 mm long, 2.5–3 mm wide, with a prominent involute wing, sparsely pubescent to glabrate. Pedicels axillary, 1.4–1.7 cm long, 1.5 mm wide, obliquely articulate 3–5 mm above the base, with persistent tightly appressed pubescence, bracteoles caducous from below articulation. Sepals 4–6 mm long, 4–6 mm wide, connate at base, subcoriaceous, broadly triangular, apex revolute, appressed-pubescent abaxially, sparsely so or glabrate adaxially. Outer petals 18–21 mm long, 7–12 mm wide, subcoriaceous, elongate-rhomboid or oblong, rounded or obtuse at apex, adaxially pubescent, hairs densest at base, abaxially pubescent, with a glabrous patch at base; inner petals 14–23 mm long, 6–9 mm wide, oblong or oblanceolate, rounded or obtuse at apex, pubescence as in outer petals. Stamens 1.2 mm long, long-trapezoidal, connectives truncate at the apex, papillate. Carpels 13–16; ovaries sericeous. Torus hemispheric, 4 mm diam., glabrate. Pedicel in fruit 1.9 cm long, 3.5 mm wide, longitudinally wrinkled and with a few small lenticels. Monocarps up to 5, the seed-containing portion 22–27 mm long, 13–14 mm wide, ellipsoid to elongate-ellipsoid, apex rounded, slightly apiculate, stipe 4 mm long, 3–4 mm wide, glabrate or with a few sparse hairs, pericarp 2 mm thick. Seed 21 mm long, 10 mm wide, ellipsoid-fusiform, dark brown, sulcate, rugulose, shiny, the exostome paler than seed coat.

Additional specimen examined. GUYANA: Upper Mazaruni River Basin, along Kako River, 25 Sep. 1960 (fl), *Tillett & Tillett 45531* (NY).

This distinctive species, a large tree with coriaceous paddle-shaped leaves and large thick-walled monocarps, is known from riverine and lower montane forest up to 800–900 m on and near Mt. Ayanganna in western Guyana. It may perhaps be expected in the eastern Venezuelan Guayana as well. It is most similar to *Guatteria dura* R. E. Fries, but that species has leaves pubescent beneath, the leaf apex rounded with a cusp 0.5–1.5 cm long, thicker petals, and monocarps with the seed-containing portion 13–17 mm long and 8–10 mm wide and with stipes 9–12 mm long.

We thank the staff of the Missouri Botanical Garden, in particular Paul Berry and Bruce Holst, for the opportunity to examine the *Guatteria* material from the Venezuelan Guayana. We also thank the curators of F, MO, NY, US, and VEN for making specimens available to us. Rupert Barneby corrected the Latin diagnoses.

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A NEW COMBINATION IN *CHASMANTHIUM* (POACEAE)

Yates (1966a, b) treated *Chasmanthium* Link as a genus distinct from *Uniola* L., based primarily on differences in embryo structure, leaf anatomy and epidermal micromorphology, and chromosome number. He recognized five species within *Chasmanthium*, *C. latifolium* (Michaux) Yates, *C. laxum* (L.) Yates, *C. sessiliflorum* (Poiret) Yates, *C. nitidum* (Baldwin) Yates, and *C. ornithorhynchum* (Steudel) Yates. During preparation of a treatment of this genus for the *Manual of North American Grasses*, it became evident to me that two of these species, *C. laxum* and *C. sessiliflorum*, were morphologically vey similar and showed significant overlap in several quantitative features, including leaf length and width, panicle length, number of florets per spikelet, and spikelet length and width. The only consistent qualitative differences between them are the pubescent leaf collars and more or less divergent panicle branches of *C. sessiliflorum* as contrasted with the glabrous leaf collars and appressed panicle branches of *C. laxum*. In addition, the two taxa are almost completely sympatric; they extend from New Jersey to Texas and Oklahoma. Given their similarities and sympatry, I feel that these two taxa are best treated as subspecies of *C. laxum* rather than as distinct species. The new combination for *C. sessiliflorum* is presented here.

Chasmanthium laxum (L.) Yates subsp. **laxum.** *Holcus laxus* L., Sp. Pl. 2: 1048. 1753. TYPE: U.S.A. Virginia: *Clayton 589* (lectotype, here designated, LINN, microfiche consulted; isolectotype, BM). *Uniola laxa* (L.) Britton, Sterns & Pogg., Prelim. Cat. 69. 1888.

Uniola gracilis Michaux, Fl. Bor. Amer. 1: 71. 1803. TYPE: "Hab. in umbrosis sylvarum, a Carolina ad Georgiam" (holotype, P not seen). *Chasmanthium gracile* (Michaux) Link, Hort. Berol. 1: 159. 1827.

Uniola virgata Bartram ex Pursh, Fl. Amer. Sept. 1: 82. 1814, nomen nudum.

Uniola uniflora Benke, Rhodora 31: 148. 1929. TYPE: U.S.A. Tennessee: Memphis, 1928, *Benke 4874* (holotype, F not seen; isotype, BM).

Chasmanthium laxum (L.) Yates subsp. **sessiliflorum** (Poiret) L. Clark, comb. et stat. nov. *Uniola sessiliflora* Poiret in Lam., Encycl. 8: 185. 1808. TYPE: "Cette plante n'a ete communiquee par M. Bosc, qui l'a recueillie dans la Caroline" (holotype, P not seen; isotype, US fragment). *Poa sessiliflora* (Poiret) Kunth, Révís. Gramin. 1: 111. 1829. *Chasmanthium sessiliflorum* (Poiret) Yates, Southw. Naturalist 11: 426. 1966.

Uniola longifolia Scribner, Bull. Torrey Bot. Club 21: 229. 1894. TYPE: U.S.A. Georgia: De Kalb Co., Little Stone Mountain, 1893, *Small s. n.* (lectotype, here designated, US).

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THE SOUTH AMERICAN *EREMODRABA* (BRASSICACEAE)

Eremodraba O. E. Schulz was originally described as a monotypic genus (Schulz, 1924) that was considered to be closely related to *Stenodraba* O. E. Schulz, *Alpaminia* O. E. Schulz, *Pelagatia* O. E. Schulz, and *Weberbauera* Gilg & Muschler (Schulz, 1936). The last four genera have been critically evaluated by Al-Shehbaz (1990); there I concluded that all four constitute a well defined, monophyletic genus recognized under the earliest name, *Weberbauera*.

The recognition of *Eremodraba* as a distinct genus is strengthened by the discovery of *E. schulzii*. The genus consists of glabrous annuals with sagittate-amplexicaul cauline leaves, conspicuously flattened fruits, yellow flowers, and filaments with papillose, dilated bases. In my opinion, *Eremodraba* is unrelated to *Weberbauera*. The latter includes cespitose, usually pubescent perennials with petiolate or sessile leaves that are neither sagittate nor amplexicaul, terete or slightly flattened fruits, white flowers, and glabrous filaments. *Eremodraba* apparently has no close relatives. It resembles only superficially the Peruvian monotypic *Dictyophragmus* O. E. Schulz that differs from *Eremodraba* in having conspicuously nerved septa, broadly winged seeds, and accumbent cotyledons.

Eremodraba was erroneously reported as suffrutescent herbs (Schulz, 1924; Macbride, 1938). There is a poor representation of the genus among the holdings of the major herbaria consulted. Both species of *Eremodraba* are apparently very rare and are restricted to mid altitudes in the deserts of nothern Chile and southern Peru. The following account aims to provide the basis for a better understanding of this very rare genus.

Systematic Treatment

Eremodraba O. E. Schulz, Pflanzenreich IV. 105(Heft 86): 362. 1924. TYPE: *E. intricatissima* (Philippi) O. E. Schulz.

Glabrous, somewhat fleshy annual herbs; stems much branched above. Cauline leaves auriculate to sagittate-amplexicaul. Inflorescences ebracteate, corymbose racemes, elongated considerably in fruit. Sepals oblong, glabrous, nonsaccate at base, erect to spreading. Petals yellow, spatulate. Stamens 6; filaments dilated and papillose at base; anthers oblong. Nectar glands confluent, subtending the bases of all stamens. Fruits oblong-lanceolate, dehiscent, flattened parallel to the septum, glabrous, straight or falcate; septum complete; stigma capitate, much broader than style. Seeds oblong, uniseriate to subbiseriate; cotyledons incumbent.

Key to the Species of *Eremodraba*

Fruits straight; fruiting pedicels divaricate, straight, 6–8 mm long; rachis of infructescence straight ..... 1. *E. schulzii*

Fruits falcate; fruiting pedicels reflexed, strongly curved, 2–3.5(–5) mm long; rachis of infructescence strongly geniculate ..... 2. *E. intricatissima*

1. Eremodraba schulzii Al-Shehbaz, sp. nov. TYPE: Peru. Depto. Arequipa: Yura, 2,500 m, 18 May 1957, *R. Hirsch P508* (holotype, GH). Figure 1.

Herba annua glabra; folia basales pinnatisecta, breve petiolata; folia caulina sessilia, integra vel dentata, sagitta-to-amplexicaula; racemi ebracteati; sepala oblonga, erecta, 2.5–3 mm longa; petala flava, spathulata, 3–4 mm longa; filamentae a basi papillosae; pedicelli fructiferi divaricati, recti, 6–8 mm longi; siliquae anguste oblongo-lanceolatae, compressae, rectae, 11–17 mm longae, 2–2.5 mm latae; stylus 0.2–0.3 mm longus; semina oblonga, 1.1–1.2 mm longa, 0.6–0.7 mm lata.

Annual herbs, glabrous throughout. Stems erect, branched above, 1–6 dm high. Basal leaves not rosulate, petiolate, pinnatisect, 4–7 cm long; lateral lobes oblong to linear, 0.5–2 cm long, 0.5–2 mm wide. Upper cauline leaves narrowly linear, strongly sagittate-amplexicaul at base, entire to dentate or rarely pinnatisect, 2–3.5 cm long, 0.5–1.5 mm wide. Inflorescences ebracteate, corymbose racemes, elongated considerably in fruit; rachis of infructescence straight. Sepals oblong, erect, scarious at margin, glabrous, 2.5–3 mm long, 1–1.3 mm wide. Petals yellow, spatulate, attenuate to clawlike base, 3–4 mm long, 0.7–1 mm wide. Filaments erect, dilated and papillose at base, 2–2.5 mm long; anthers ovate, 0.5–0.6 mm long. Fruiting pedicels divaricate, straight, glabrous, 6–8 mm long. Fruits narrowly oblong-lanceolate, flattened parallel to septum, straight, 11–17 mm long, 2–2.5 mm wide; valves glabrous, obscurely nerved, acute-acuminate at apex, obtuse at base; septum complete; style 0.2–0.3 mm long; stigma capitate,

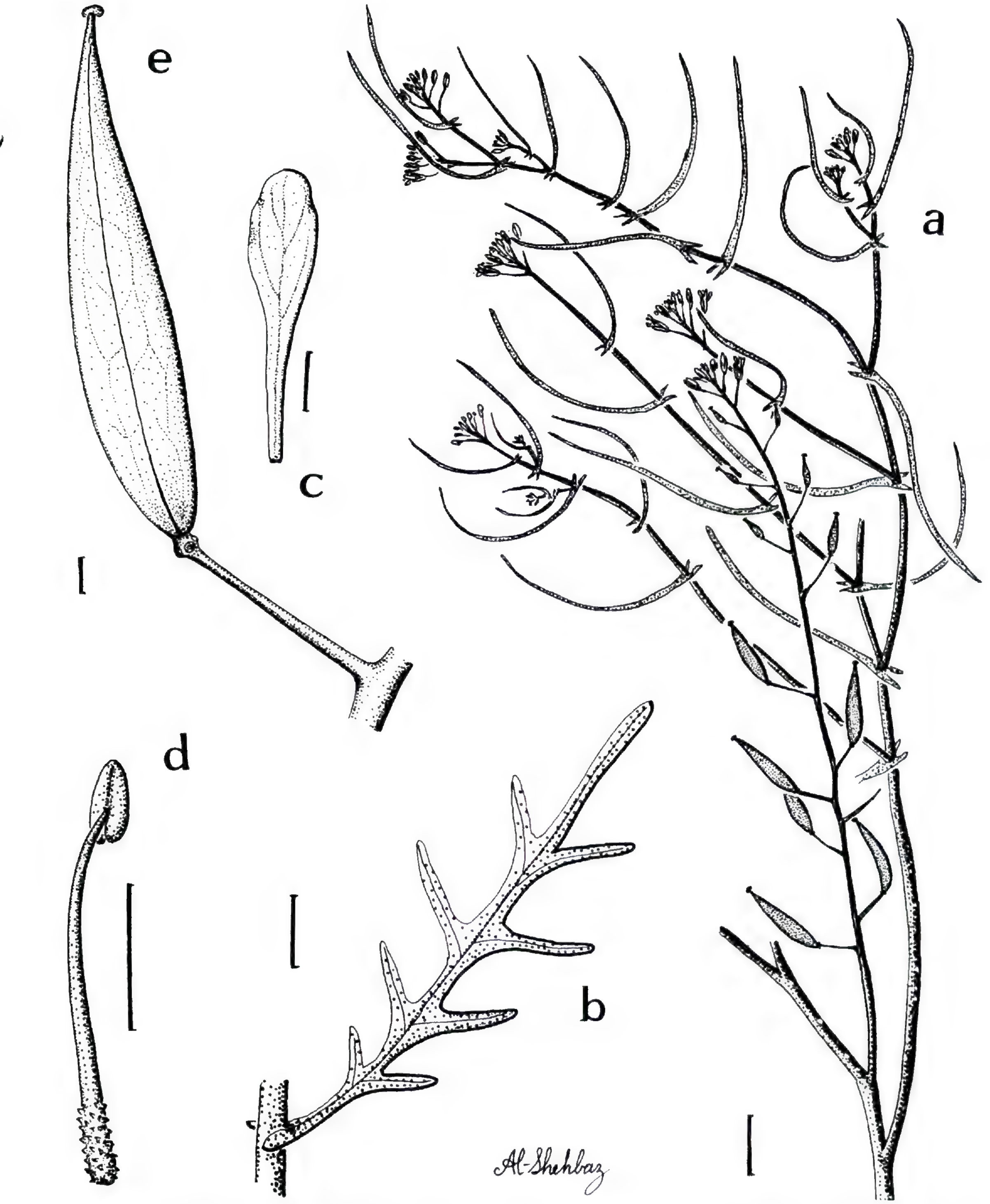

FIGURE 1. *Eremodraba schulzii.* —a. Portion of plant.—b. Lower cauline leaf.—c. Petal.—d. Stamen.—e. Fruit. Scales a, b = 1 cm; c–e = 1 mm. Drawn from the holotype except b, which was drawn from *Sandeman 3944*.

much wider than style. Seeds oblong, somewhat biseriately arranged, 1.1–1.2 mm long, 0.6–0.7 mm wide; cotyledons incumbent.

Additional specimens examined. PERU. DEPTO. AREQUIPA: southern slope of Chachani Mt., 3,050 m, *Hinckley 70* (B, GH); near the old road from Arequipa to Mollendo, *Sandeman 3944* (OXF).

Eremodraba schulzii, named in honor of Otto Eugen Schulz (31 Oct. 1874–17 Feb. 1936), an outstanding student of the Brassicaceae, was first named by Schulz (1936) as "*E. ? hinckleyana.*" However, the latter name was invalidly published because it was not accompanied by Latin description or diagnosis. Furthermore, Schulz treated *Eremodraba* as monotypic and was doubtful in his assignment of *E. hinckleyana* to the genus because the material examined had no fruits. I have described the species as new and chose a type with fruits and seeds, rather than to validate Schulz's name, which was based on a flowering material.

2. Eremodraba intricatissima (Philippi) O. E. Schulz, Pflanzenreich IV. 105(Heft 86): 363. 1924. *Draba intricatissima* Philippi, Anal. Mus. Nac. Chile Bot. 8(2): 5. 1891. *Sisymbrium intricatissimum* (Philippi) Reiche, Fl. Chile 75. 1895. *Hesperis intricatissima* (Philippi) Kuntze, Revis. Gen. Pl. 3(2): 5. 1898. TYPE: Chile. [Región I] Tarapacá (as province): between Mocha and Guavina, *C. Rahmer s.n.*, 12 Mar. 1885 (holotype, SGO 63194 seen).

Annual herbs, glabrous throughout. Stems erect, much branched above, 1–5 dm high. Lowermost leaves not seen; middle and upper cauline leaves somewhat fleshy, oblong to linear, auriculate to sagittate-amplexicaul at base, usually entire, 0.7–5 cm long, 1–4 mm wide. Inflorescences ebracteate, corymbose racemes, elongated considerably in fruit; rachis of infructescence conspicuously geniculate. Sepals glabrous, oblong, erect to spreading, caducous or persistent, scarious at margin, 1.8–2 mm long, 0.9–1 mm wide. Petals spatulate, yellow, 2.5–3 mm long, 0.5–0.8 mm wide. Filaments dilated and papillose at base, 1.5–2 mm long; anthers ovate, 0.6–0.7 mm long. Fruiting pedicels strongly curved, reflexed, 2–3.5(–5) mm long. Fruits oblong-lanceolate, falcate, flattened parallel to the septum, (3–)5–10(–14) mm long, 1.5–2 mm wide; valves glabrous, obscurely nerved; septum complete; style 0.1–0.2(–1) mm long; stigma capitate, much broader than style. Seeds oblong, uniseriate to subbiseriate, 1.2–1.3 mm long, 0.6–0.7 mm wide; cotyledons incumbent.

Additional specimens examined. CHILE: [Región I] Tarapacá (as province), Pica, 1,400 m, *Werdermann 751* (E, G, GH, MO, UC); Depto. Tarapacá (now province Iquique), Noasa-Mamina, 2,700 m, *Werdermann 1573* (NY); Tarapacá, *Philippi s.n.*, 1888 (B).

There is considerable variation in the orientation and duration of sepals and in the length of fruits of *Eremodraba intricatissima*. Because of the scarcity of material at my disposal, I have refrained from recognizing these variants formally.

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BOOK REVIEW

Yungjohann, John C. (edited by G. T. Prance, with an epilogue by Yungjohann Hillman). White Gold, the Diary of a Rubber Cutter in the Amazon 1906–1916. Synergetic Press, P.O. Box 689, Oracle, Arizona 85623, U.S.A. 1989. Frontispiece + 103 pp., illus., ISBN 0-907791-16-6. Retail price: $7.95.

Not a diary in the sense of a day-by-day log, *White Gold* is an account of the experiences of New York native John Yungjohann's ill-advised plunge into the upper Amazon as a rubber tapper. Ghillean Prance edited the first-hand text lightly, and augmented it with an introduction that lends perspective. Using a glossary and notes, he defined terms, identified plants and creatures, and clarified obscure points. Numerous black and white photographs taken by Dr. Prance and a map enrich the book.

John Yungjohann made his way up the Amazon and Rio Purus to the mouth of the Rio Xapuri in far-western Brazil. Here a series of surprises began when he was trapped into the purchase of excess supplies at inflated prices and teamed up with six companion tappers and a guide of dubious character. The next surprise was that the work area "a couple of hours" up the river turned out to be 45 days up the river. After teaching the team the basics, the guide disappeared. Before long all seven adventurers were malarial, with the outcome that the hero, himself near death, variously disposed of the remains of his less fortunate companions. He survived and more or less flourished until beriberi forced him to abandon a subterranean treasure trove of rubber and return to New York, where he resumed his interrupted career as a tilesetter.

This is no place to summarize the plot. Suffice it to note that Mr. Yungjohann described rubber tapping, malaria, the experience of being discovered living alone by the local Indians (who turned out to be most hospitable), a system of enslaving rubber tappers through debt, wildlife encounters, and a series of incredible adventures. The book reads like a novel, and there is even a (very brief) romance, in which boy did not get girl.

The only flaw is that the story is intriguing and sketchy at the same time, leaving the reader hungry for more. It is thoroughly pleasing, easy reading, and would make a good supplement to a high school or college course that deals with economic plants or the Amazon, especially with the ecology and economy of the region in the news, and with the tragedy of Chico Mendes a fresh memory. Any person interested in these subjects or neotropical botany, rubber, tropical diseases, human nature, or adventure will find the book a delight. Plan on reading it in one sitting.—George K. Rogers, *Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A. Present address: Cox Arboretum, 6733 Springboro Pike, Dayton, Ohio 45449, U.S.A.*

Volume 77, Number 2, pp. 225–425 of the ANNALS OF THE MISSOURI BOTANICAL GARDEN was published on May 1, 1990.

Rolf Dahlgren
(1932–1987)

Systematics and Evolution of the Monocotyledons

The following seven papers were part of the symposium *Systematics and Evolution of the Monocotyledons*, which was sponsored by the American Society of Plant Systematists and the Systematics Section of the Botanical Society of America and was held at the American Institute of Biological Sciences meetings at the University of Massachusetts, Amherst, August 1986.

The publication of these proceedings is supported in part by National Science Foundation grant BSR-9005141.

The symposium papers are dedicated to the memory of Rolf Dahlgren, noted student of monocot systematics and evolution.

New Publications from the Missouri Botanical Garden

Thesaurus Dracularum, 3

Ortyle A. Luer, with German translations by Fritz Hamer. Watercolor paintings by Stig Dalström. 1990.

Thesaurus Dracularum is a popular monograph of the orchid genus *Dracula*. Each of the 80-odd known species is illustrated by a watercolor painting accompanied by descriptions, discussions, and distributions in both English and German, with distribution maps and black and white line drawings. In elephant format. Standing orders available. The third of six fascicles (fascicles 1 and 2 are also available at the price listed here). U.S. orders, $40 each, postage paid; non-U.S. orders, $42, postage paid.

Index to Plant Chromosome Numbers 1986–1987

Edited by Peter Goldblatt and Dale E. Johnson. Monograph in Systematic Botany from the Missouri Botanical Garden, Number 30. 1990.

The *Index to Plant Chromosome Numbers* is compiled by an international committee and collated and edited by Peter Goldblatt and Dale E. Johnson, Missouri Botanical Garden. It is indispensible to those engaged in a variety of botanical studies, ranging from systematics and evolution to plant breeding, forestry, and horticulture. Counts for all plant groups—algae, fungi, bryophytes, pteridophytes, and spermatophytes—are included and arranged alphabetically by family, genus, and species. Each count includes the name of the taxon as used in the original report, the number reported, and reference to the original report. References are contained in a bibliography that contains citations at the level of about 500 per year. 243 pages. $15, plus postage.

Botanical Research and Management in Galápagos

Edited by J. E. Lawesson, O. Hamann, G. Rogers, G. Reck and H. Ochoa. Monograph in Systematic Botany from the Missouri Botanical Garden, Number 32. 1990.

The volume contains the proceedings of the International Workshop on Botanical Research and Management in Galápagos, organized by the Charles Darwin Research Station and the Galápagos National Park Service, held in April 1987 at the Charles Darwin Research Station, Santa Cruz, Galápagos, Ecuador. The 34 papers contained in this book discuss various aspects of conserving and managing the Galápagos flora and vegetation. 297+ pages. Soft cover. Illustrated. $30, plus postage.

Glossarium Polyglottum Bryologiae, A multilingual glossary for bryology

Edited by R. E. Magill. Monograph in Systematic Botany from the Missouri Botanical Garden, Number 33. 1990.

This polyglot glossary provides definitions for nearly 1,200 terms in four languages—English, French, German, and Spanish. In addition, all English terms are translated into Japanese, Latin, and Russian. This volume will be important to professionals, nonprofessionals, and students as a means of learning the specialized vocabulary of bryology and interpreting the varying usages of terms. 297 pages. Paper cover. $12, plus postage.

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Cover illustration. *Sisymbrium ilutasii* Al-Shehbaz, by Ihsan A. Al-Shehbaz.

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PHYLOGENY AND CLASSIFICATION OF IRIDACEAE[1]

Peter Goldblatt[2]

ABSTRACT

A cladistic analysis of Iridaceae, a family of some 1,630 species and ca. 77 genera, and the closely allied *Geosiris* and *Isophysis*, both monotypic and sometimes accorded family status, suggests a phylogeny in which there are four major lineages, recognized as subfamilies. Characters used in the analysis include vegetative and floral morphology, anatomy, embryology, pollen ultrastructure, chromosome cytology, and flavonoid and amino acid chemistry. Isophysidoideae, with a superior ovary, include only the Tasmanian *Isophysis*. Nivenioideae include the Afro-Madagascan *Aristea*, three woody Cape genera, the Australasian *Patersonia*, and *Geosiris*. The last-mentioned, a saprophyte, restricted to Madagascar, appears to be most closely related to *Aristea* and is not recognized at the tribal level. Iridoideae have four reasonably well differentiated tribes and a worldwide but predominantly southern distribution. The subfamily is specialized in floral and phytochemical features. Ixioideae, which comprise slightly more than half the total species of Iridaceae, are predominantly southern African and have derived leaf anatomy, pollen exine, flavonoids, and inflorescences. Three tribes are recognized in Ixioideae and four in Iridoideae in both of which some subtribal groupings are suggested. Described formally here are Nivenioideae and Pillansieae.

Iridaceae are a relatively large family of petaloid monocots (Liliiflorae sensu Dahlgren et al., 1985) comprising over 1,630 species in ca. 77 genera. Although distributed worldwide, the family has a marked concentration on the southern continents and the major center of radiation in Africa south of the Sahara. Iridaceae are easily recognized among the monocots by having isobilateral equitant leaves, flowers with three stamens, and, with the exception of the monotypic Tasmanian *Isophysis*, an inferior ovary. *Isophysis* (Fig. 1A) has in the past been assigned variously to Isophysidaceae, Hypoxidaceae, or Liliaceae–Melanthioideae as well as to Iridaceae (Goldblatt et al., 1984). Such is the morphological distinctness of Iridaceae that there is virtually no controversy over their status and circumscription, except for the treatment of *Isophysis* and the monotypic saprophyte *Geosiris* from Madagascar, both of which have been regarded as separate families (Jonker, 1939).

[1] Supported by grants DEB 78-10655 and DEB 81-19292 from the U.S. National Science Foundation. I thank James Walker for encouraging me to undertake this study; Bruce L. Stein for assistance with the cladistic analysis; Paula Rudall, Christine Williams, and B. L. Burtt for their helpful comments on the manuscript and in its preparation; and Margo Branch and John Myers for the original illustrations used here.

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Iridaceae are usually assigned to the order Liliales (the definition of which varies considerably) but have also been treated in Iridales, either alone (Hutchinson, 1934, 1973), or with Geosiridaceae, Burmanniaceae, and Corsiaceae (Takhtajan, 1969). The unanimity of opinion concerning the status and circumscription of Iridaceae has largely obscured any critical appraisal of the relationships of this family. Colchicaceae (Liliaceae–Melanthioideae in part) have been suggested as immediately allied to Iridaceae (Takhtajan, 1969, 1980), and Takhtajan (1980, 1985) has allied Iridaceae with Tecophilaeaceae in suborder Iridineae, a relationship first espoused by Hutchinson (1934) but discounted by Goldblatt et al. (1984). Dahlgren & Rasmussen (1983) have allied Iridaceae with the Pacific family Campynemataceae and the two to Colchicaceae. New evidence (Goldblatt et al., 1984; Goldblatt, 1986b) now makes this also seem untenable.

Infrafamilial phylogeny and classification of Iridaceae, the emphasis of this paper, have varied with each major treatment of the flowering plants (or monocots alone), but most systems have consistently accepted the existence of one of the main subfamilial categories, subfamily Ixioideae (tribe Ixieae of Bentham & Hooker, 1883; Diels, 1930). There has been little agreement, however, over the circumscription and rank of the other half of the family, here treated as subfamilies Isophysidoideae, Nivenioideae, and Iridoideae. Bentham & Hooker (1883) admitted two more tribes (their major infrafamilial category), Moraeeae (now Irideae) and Sisyrinchieae, the latter including genera here referred to subfamilies Iridoideae and Nivenioideae. The rather different treatment of Pax (1888) recognizes the two major subfamilies admitted here, Ixioideae and Iridoideae (the latter including Nivenioideae as a tribe) and a third, Crocoideae, for four acaulescent genera, *Romulea*, *Syringodea*, *Crocus*, and *Galaxia*, now confidently referred either to Iridoideae or Ixioideae (Goldblatt, 1971). The treatment of Iridaceae by Hutchinson (1934, 1973) is similar to that of Bentham & Hooker but admits 11 tribes, essentially recognizing each of Bentham & Hooker's three tribes and subtribes at the same rank. Hutchinson was, however, the first to include *Isophysis* in Iridaceae, as the only member of Isophysideae.

Recent treatments of Takhtajan (1980: 310) and Thorne (1983) include *Geosiris* in Iridaceae as a subfamily, Takhtajan also including *Isophysis* and Campynemataceae (see Dahlgren et al., 1985) in Iridaceae as subfamilies. The recent and thorough studies of the monocots by Dahlgren and coworkers recognize Geosiridaceae as distinct from Iridaceae, the latter (Dahlgren et al., 1985) including five subfamilies, Isophysidoideae, the nomen nudum Aristeoideae (Nivenioideae here), Sisyrinchioideae, Iridoideae, and Ixioideae.

This paper represents the first objective phylogenetic classification of Iridaceae using modern cladistic methods. It is also the first to use data extensively from fields other than morphology, adapting information from chromosome cytology, flavonoid and amino acid chemistry, anatomy, and pollen morphology. The results confirm that *Isophysis* is probably best included in Iridaceae in a separate subfamily Isophysidoideae and suggest that *Geosiris* be included in Iridaceae–Nivenioideae.

Methods of Analysis

Cladistics affords the most objective and critical method of assessing phylogeny, and the results of my cladistic analysis of Iridaceae are presented in the following pages in several cladograms. The cladograms (Figs. 3–5) were constructed manually following concepts of grouping by shared derived characters (synapomorphies) established by Hennig (1966) together with the principle of parsimony as adapted by several botanists (Bremer, 1976; Funk, 1982; Dahlgren & Bremer, 1985; Goldblatt, 1985). The manually generated cladograms were tested using the PAUP Program (Swofford, 1985), which produced the same results.

The polarities of the characters were determined either by outgroup comparison or following widely accepted general character trends in the monocots or flowering plants. The characters used for the cladistic analysis are discussed in detail below, and are outlined in Table 1.

Anatomical data are taken from studies by Cheadle (1963) and Rudall (1983, 1984, 1986) and pollen data from the extensive studies of Schulze, summarized in 1971 (Schulze, 1971). Flavonoid data have only recently become available and information is adapted from a wide survey by Williams et al. (1986). Other important phytochemical data are from studies by Larsen et al. (1981, 1987). Chromosome cytology is comparatively well known for Iridaceae, but the unusually variable karyological data are of limited use above subtribal levels owing to the difficulty in establishing basic numbers for higher ranks.

The characteristics of the families and orders of the Liliiflorae are taken largely from the several recent works of Dahlgren and his co-workers (Dahlgren & Clifford, 1982; Dahlgren & Rasmussen, 1983; Dahlgren et al., 1985; Dahlgren & Bremer, 1985).

Circumscription of Tribes

Given the present state of our knowledge, it is impractical to deal with individual genera of Iridaceae for this type of analysis. Instead, I have chosen apparently natural generic groups (sometimes corresponding to tribes or subtribes) as working taxonomic units. It is clear that three of the four tribes of Iridoideae—Irideae, Mariceae, and Tigrideae—are natural and monophyletic groups, while the nature of the fourth, Sisyrinchieae, is less certain. Although it may be an unnatural alliance, for the purposes of this study it is regarded as monophyletic, and the data so far accumulated support this. However, an important question still remains as to whether *Orthrosanthus* and *Libertia* (both Pacific and South American) and *Bobartia* (South African) are in fact related to the core genera of Sisyrinchieae (all New World).

Nivenioideae may also be found to be unnatural, but no convincing data have yet come to light that indicate an alternative treatment. In Ixioideae I had no preconceived ideas about tribal groupings when I undertook this study, but Watsonieae have emerged as a tribe distinct from Ixieae, which still comprise a large number of genera that may in the future be found to be better treated in more than one tribe. It also became clear from the preliminary analysis that the monotypic *Pillansia* is very isolated in Ixioideae and probably the sister group of the rest of the subfamily (Fig. 5). It is referred to a monotypic tribe, a decision that could not be avoided.

Geosiris has all the derived states of Nivenioideae as well as some of its own, and according to the data available, is the sister genus of *Aristea*. *Isophysis* merits its own subfamily, and in this analysis emerges as the sister taxon of the rest of the Iridaceae. I must, however, emphasize that the embryology of both *Isophysis* and all Nivenioideae except *Geosiris* (Goldblatt et al., 1987) is unknown, and has been assumed to correspond with *Geosiris* (presence of a parietal cell in the ovule; secretory tapetum; successive microsporogenesis; helobial endosperm development) and not the embryologically better known Iridoideae and Ixioideae, which appear to be specialized in having simultaneous microsporogenesis and nuclear endosperm formation (the polarity of these two characters is uncertain). *Geosiris* and *Isophysis* have not been examined for free amino acids.

Character Analysis

The features of systematic and phylogenetic significance are presented below under headings of Morphology, Embryology, Cytology, Anatomy, and Phytochemistry. Only the more important characteristics are discussed at length. The reasons for assigning character polarities are indicated unless they are self-evident. The data are summarized in Table 1 and are used in the construction of the cladograms (Figs. 3–5).

MORPHOLOGY

Rootstock. The basic type of rootstock in Iridaceae is almost certainly a creeping persistent rhizome; bulbs and corms are independently derived from a rhizome. All members of Tigrideae have a bulb covered by dry brownish tunics. Elsewhere in the family, bulbs occur in *Iris* subgenera *Scorpiris*, *Xiphion*, and *Reticulata*, and they may have evolved independently in each (Mathew, 1981, and pers. comm.).

Corms are basic in Ixioideae and also occur in the several African genera of Irideae subtribes Homeriinae and Ferrariinae (Lewis, 1954; Goldblatt, 1976). In Ixioideae (Fig. 8) the corms have a distinct stele, produce roots from the base, and are usually composed of several internodes (Lewis, 1954; de Vos, 1977; Goldblatt, 1982a). Development proceeds in two different ways. In Watsonieae and Pillansieae the corm is formed entirely from an axillary bud (*Watsonia*-type sensu de Vos, 1977) at the base of the terminal flowering stem, and the corm's shoot primordium is apical. In Ixieae, by contrast, the corm develops at least partly from the base of the flowering stem (*Ixia*-type of de Vos, 1977), and a bud in the axil of the upper node of the corm produces the following season's growth. In the *Watsonia*-type the new corm is attached to the base of the flowering stem and thus lateral to it, and in the *Ixia*-type the new corm is basal to the flowering stem, and situated below its insertion.

In both cases the flowering axis is terminal and the growth pattern is sympodial and analogous to the sympodial growth of a rhizome where the flowering stem is terminal and buds lateral to it continue the next growth flush. The *Ixia*-type of corm appears to be derived and is here regarded as the major synapomorphy uniting the genera assigned to Ixieae.

In Irideae the corms have a diffuse stele (de Vos, 1977), produce roots (Fig. 6) from the apical bud (Goldblatt, 1987), and, except in *Ferraria* (only genus of Ferrariinae), are of a single internode. The *Homeria*-type corm is a major synapomorphy for this large subtribe of Irideae.

Leaves. The basic leaf type is ensiform and isobilateral (Arber, 1921) with an open sheathing

TABLE 1. Characters used in the cladograms (Figs. 3–5). The derived (apomorphic) states are listed first followed by the presumed ancestral (plesiomorphic) condition. Characters believed to have evolved independently (parallelisms) are indicated by double lines in the cladograms. Although characters 31 and 45 did not ultimately contribute to the cladograms, they were included in the study and hence remain in the table.

	Apomorphic states	Presumed ancestral conditions
	MORPHOLOGICAL CHARACTERISTICS	
1.	Rootstock a bulb	Rootstock a persistent creeping rhizome
2.	Rootstock a corm of several internodes	Rootstock a persistent creeping rhizome
3.	Corm partly apical in origin and basal to the flowering stem	Corm axillary in origin and lateral to the flowering stem
4.	Leaves ensiform and equitant	Leaves bifacial
5.	Leaves plicate	Leaves flat
6.	Leaf sheaths closed	Leaf sheaths open
7.	Inflorescence consisting of one or more rhipidia, each enclosed in large spathes	The unspecialized condition is uncertain and will remain so until a specific outgroup has been identified
8.	Rhipidia single-flowered	Rhipidia several to few-flowered
8A.	Rhipidia binate	Rhipidia single
9.	Flower sessile	Flowers pedicellate
10.	Inflorescence a spike	Inflorescence not a spike
11.	Flowers fugacious	Flowers lasting at least two days
12.	Flowers blue	Flowers shades of yellow to orange
13.	Tepals clearly divided into a limb and broad claw	Tepals not clawed
14.	Tepals united in a tube	Tepals free
15.	Stamens three (outer whorl absent)	Stamens six in two whorls
16.	Filaments weak, anthers adhering to the style branches	Filaments supporting free anthers
17.	Pollen grain exine micropunctate (punctitegillate)	Exine reticulate
18.	Stem unbranched	Stem branched
19.	Ovary inferior	Ovary superior
20.	Style deeply three-forked to below the base of the anthers and each division conduplicate and terminally stigmatic	Style lobed or divided above the anthers and each branch stigmatic along its entire length
21.	Style arms extended between the stamens	Style arms parallel to and appressed to the stamens
22.	Style branch apices produced into erect paired appendages (crests) above, stigmatic only below	Style branch apices symmetrical and uniformly stigmatic
23.	Style branches thickened and somewhat compressed radially	Style branches slender and symmetric
24.	Style branches flattened and petaloid (compressed tangentially)	Style branches slender and symmetric
25.	Style branches deeply forked	Style branches undivided or apically forked
26.	Nectaries perigonal	Nectaries septal
27.	Perigonal nectaries restricted to the base of the outer tepals	Nectaries located on inner and outer tepals
28.	Perigonal nectaries most strongly developed on the inner tepals	Nectaries located on inner and outer tepals
29.	Nectaries secreting oil from special elaiophores	Nectaries secreting only sugars
30.	Nectaries lacking	Nectaries present
	ANATOMICAL CHARACTERS	
31.	Styloid crystals in vascular bundle sheaths and other tissues	Raphides present and styloids absent
32.	Vessel perforations simple	Vessel perforations scalariform
33.	Primary thickening meristem (PTM) reduced and pericyclic vasculature scant	PTM and pericyclic vasculature more or less extensive
34.	Distinct midrib in leaf vein	No single major leaf vein present
35.	Leaf margins with subepidermal sclerenchyma	Marginal subepidermal sclerenchyma not developed
36.	Mesophyll cells elongated across the horizontal axis	Mesophyll cells ± isodiametric or longitudinally elongated
37.	Epidermal cells with sinuous walls	Epidermal cells with ± straight walls
38.	Epidermal cells with two–few papillae	Epidermal cells with one or no papillae

[There is no character 39.]

TABLE 1. Continued.

Apomorphic states	Presumed ancestral conditions
PHYTOCHEMICAL CHARACTERS	
FLAVONOIDS	
40. Flavonols absent	Flavonols abundant
41. Flavones present	Flavonols present
42. Mangiferin (xanthone *C*-glycoside) often present	Mangiferin absent
43. Flavonol *O*-glycosides predominant (to exclusive)	Flavone *C*-glycosides predominant
44. Flavone *C*-glycosides absent	Flavone *C*-glycosides present
45. Flavone *O*-glycosides accumulated	Flavonol *O*-glycosides and/or flavone *C*-glycosides present
46. Flavonol sulfate present	Flavonol sulfate absent
47. Biflavones absent	Biflavones present
FREE AMINO ACIDS AND PEPTIDES	
48. Free meta-carboxyphenylalanine and carboxyphenylglycine present	These compounds absent
49. Gamma-glutamyl peptides produced	Absent
[There is no character 50.]	
EMBRYOLOGICAL AND KARYOTYPIC CHARACTERS	
51. Microsporogenesis simultaneous	Microsporogenesis successive
52. Endosperm formation nuclear	Endosperm formation helobial
53. $x = 7$	$x = 10$

base. Depending on the choice of outgroup for the family, the equitant leaf may or may not be derived. Among possible immediate ancestors of Iridaceae, several genera of Melanthiaceae (Melanthiales sensu Dahlgren et al., 1985) have similar leaves, notably Tofieldieae, but dorsiventral leaves are basic for the core families of Liliales (e.g., Dahlgren & Rasmussen, 1983). Important modifications of the basic equitant leaf are the pleated (foliated) leaves of Tigridieae, the synapomorphy that unites the tribe, together with the bulbous rootstock. Plicate leaves also occur in some Ixioideae, notably *Babiana* and most *Crocosmia* species, and appear to have evolved repeatedly in this subfamily. Secondarily bifacial and dorsiventral leaves have evolved in several genera, most significantly in the largely African Irideae–Homeriinae (Fig. 6). This leaf type and an apically rooting single-internode corm define the subtribe. Similar bifacial leaves may also be basic for *Iris* subgenera *Scorpiris*, *Xiphium*, and *Reticulata*, all of which also have bulbs. In Ixioideae, *Crocus* and the closely related southern African *Syringodea* have dorsiventral leaves. Closed leaf sheaths are a feature of Ixioideae and are scattered in Iridoideae but are probably not basic in the latter.

Inflorescence. The basic inflorescence is probably the distinctive so-called rhipidium, a specialized monochasial cyme. There can be no doubt that its distinctive structure comprises at least one (as treated here) and perhaps three separate synapomorphic states if the spathelike sheathing bracts and the collapsed axis are considered separately from the arrangement of the flowers. All Iridoideae have rhipidia either terminal on the main and lateral branches in a variously elaborated paniculate arrangement, or there may be only one or a few rhipidia clustered terminally. The rhipidia consist of two large bractlike sheathing green spathes enclosing a few or sometimes several pedicellate flowers, these essentially attached at a single point. Each flower has a basal bract which also encloses all the younger buds. The flowers are raised successively out of the spathes over a period of a week or more depending on their number. The two rhipidal spathes are probably best interpreted as the outer representing the subtending bract of the inflorescence and the inner the bract of the first flower.

Variously fused rhipidia, usually paired (binate) (Weimarck, 1939), characterize all genera of Nivenioideae. In *Isophysis* (Fig. 1A) the flower is solitary but enclosed in what appear to be the opposed spathes typical of an iridaceous rhipidium. The single-flowered state is presumed to be a derived condition for the genus. In Ixioideae the flowers are always sessile and are subtended by an outer bract and an inner bracteole, the latter a double structure like the flower bracts in the rhipidia elsewhere in the family. Each flower and its bracts are here regarded as the homologue of a rhipidium. In most genera of Ixioideae, notably excluding *Pillansia*, the flowers are arranged along a straight or slightly flexuose axis, thus constituting a spike

FIGURE 1.—A. *Isophysis tasmanica* (Hook.) T. Moore (Isophysidoideae) (from Cooke, 1986).—B. *Nivenia dispar* Ecklon ex Baker (Nivenioideae), showing woody stem, compound inflorescence, flower, fruiting branch and detail of ovary. Habits ×½, details life size or variously enlarged.

(Fig. 8). In *Pillansia* the flowers are arranged in a panicle, the presumably ancestral condition. *Pillansia* is unspecialized in several ways in relation to other Ixioideae (Fig. 7). A few Ixioideae have a reduced spike, sometimes a single flower, notably *Romulea*, *Syringodea*, and *Crocus*, where the flowers are solitary, or solitary on each branch of the flowering stem.

The flower. The iridaceous flower is variable in color, size, and form, and it is difficult to treat the considerable variation in formal primitive or advanced states for higher categories. The flower is trimerous with a major synapomorphy for the family the loss of the inner whorl of stamens. Except for *Isophysis*, the ovary is inferior (Fig. 1A), and it seems reasonable to regard this specialization as fundamental to the success and radiation of the rest of Iridaceae. However, with the inclusion of *Isophysis*, the inferior ovary is not a family synapomorphy. The inferior ovary is assumed to have evolved only once and it is the sole synapomorphy uniting subfamilies Nivenioideae, Iridoideae, and Ixioideae. Except in Ixioideae and the specialized *Diplarrhena* (Iridoideae), the flowers are radially symmetric. The tepals are united in a developed tube (not merely basally contiguous at the apex of the ovary) in some genera or species of Nivenioideae (*Patersonia*, *Nivenia*, *Witsenia*) and Iridoideae (*Iris*, *Moraea* sect. *Tubiflora*, *Olsynium* (incl. *Chamelum*, *Phaiophleps*)), and are always united in Ixioideae.

In Ixioideae the flowers are often medianly zy-

gomorphic but the basic state for the subfamily is radial symmetry. Zygomorphy has evolved independently in several lines in Ixioideae. A perianth tube is characteristic of all Ixioideae, and the flowers are long-lived, nondeliquescent, and last at least two days, a contrast with most Iridoideae and Nivenioideae, which have fugacious and usually deliquescent flowers. Notably, *Isophysis* also has long-lasting flowers, and this state is probably the basic one for the family. According to the cladogram generated here, fugacious flowers evolved independently twice, in Nivenioideae and Iridoideae. An alternative, that it is a shared development in the line leading to Iridoideae, Nivenioideae, and Ixioideae, means that a reversal for the condition must have occurred in the ancestral Ixioideae. A cladogram with this conformation is less parsimonious by at least three steps.

Nectaries. Perigonal nectaries are considered a derived condition for the families of Liliales (Dahlgren & Rasmussen, 1983), and septal nectaries are generally accepted to be basic for the monocots. *Nivenia* and *Klattia* and probably *Witsenia*, all Nivenioideae, have septal nectaries but other members of the subfamily apparently lack nectaries altogether, as does *Isophysis* (Cooke, 1986). When nectaries are present in Iridoideae they are located on the tepals, either near the base or variously placed on the tepal surface. In Iridoideae perigonal nectaries are apparently lacking or uncommon in the least specialized Sisyrinchioideae (this requires careful checking in living material) but are present at the base of all the tepals at least in *Bobartia paniculata* G. Lewis. The nectaries are restricted to the base of the outer tepals in some specialized genera or species of Irideae (regarded as apomorphic for the tribe although absent in the relatively unspecialized *Dietes*), but some specialized species have nectaries on both inner and outer tepals (a secondary condition?). In contrast, nectaries are best developed on the inner tepals in Mariceae and Tigridieae, where they are often partly concealed by folds in the tepal lamina. In the latter two tribes the nectaries secrete oil (Vogel, 1974) from special club-shaped glands (elaiophores). Similar glands may also be present on the filaments in *Sisyrinchium*.

Septal nectaries are present in all of the many genera of Ixioideae (Daumann, 1970) so far examined and this presumably represents the basic state for the subfamily.

Stamens. An important synapomorphy for Mariceae and Tigridieae is the weak filaments that are shared by several genera of both tribes. These slender filaments do not support the anthers, which are lightly attached to the upper part of the style branches. (Some specialized genera of Tigridieae have typical sturdy filaments.) The filaments are united, either partly or completely in several Irideae and Tigridieae, but the condition is not basic in either tribe and has probably evolved more than once in each.

Pollen grains are basically monosulcate with a tectate-reticulate exine in Iridaceae (Schulze, 1971), thus conforming to the probable ancestral condition in the monocots. Ixioideae, including the taxonomically isolated *Pillansia* (Goldblatt & Stein, 1988), differ significantly in having micropunctate and usually microspinulate exine (Schulze, 1971; de Vos, 1982; Goldblatt & Stein, 1988). Nonaperturate grains occur in the specialized *Syringodea* and *Crocus*. Bisulcate grains are found in many Tigridieae, and may be a synapomorphy for subtribe Tigridiinae (Goldblatt, 1982b) although they also occur in some Cipurinae (Rudall & Wheeler, 1988). Syncolpate grains occur frequently in Iridoideae but are basic only to certain genera or species groups. Acolpate or anomatreme grains are recorded in some sections and subgenera of *Iris* (Schulze, 1971); they are not characteristic of any generic groups.

Style. Basic style and stigma structure is presumed to be the condition found in *Isophysis* and Nivenioideae, in which the branches or lobes are relatively short and stigmatic along the entire upper surface. Many Iridoideae differ in having long style branches (Fig. 2A), often exceeding the style, the margins of which are convolute so that the style branch is tubular and thus stigmatic only terminally. This modified structure is further specialized in Irideae, Mariceae, and several (presumably basal) genera of Tigridieae, apparently in a similar way. The apices of the style branches are produced above as a pair of flat, erect, nonstigmatic appendages, while the stigmatic surface is confined to the lower part (Fig. 6A).

In Irideae the style branches are, in addition, flattened and petaloid, and the stigmatic surface is often a small lobe restricted to the median ventral surface. In Mariceae and many Tigridieae the style branch is substantially thickened, and the stigma lobe often has a second pair of erect appendages similar to but smaller than the appendages at the upper apices of the style branches. Accompanying this are the weak filaments that do not support the anthers, which are lightly attached to the upper part of the style branch below the stigmatic surface. An elaborate style branch organization is not found

FIGURE 2. Iridoideae, tribes Sisyrinchieae and Tigridieae.—A. *Libertia chilensis* (Mol.) Gunkel, habit and detail of stamens and gynoecium.—B. *Sisyrinchium arenarium* Pöppig, habit and detail of stamens and gynoecium.—C. *Alophia drummondii* (Graham) R. Foster, habit and details of flower, fruit, and stamens and gynoecium (A, B from Correa, 1969). Habits ×½, details life-size or variously enlarged.

in all genera of Irideae and Tigridieae. The branches may be secondarily reduced and simplified in some genera, sometimes, as in *Eleutherine* and *Calydorea* (Tigridieae) and *Roggeveldia* (Irideae), to long filiform arms, or completely divided into paired and usually slender lobes (*Nemastylis*, *Alophia*, *Tigridia*—Tigridieae; *Hexaglottis*—Irideae).

A possible synapomorphy for Sisyrinchieae is the orientation of the long filiform style branches between, rather than opposite, the stamens (Fig. 2A), the latter being basic for the family. Although this may be a weak character, it is treated here as the synapomorphy that unites this tribe. The only other specialized condition that the genera apparently share is the absence of flavonols, another weak synapomorphy, and one also found in Maricaeae and Tigridieae.

Fruit and seed. Loculicidal capsules, presumably derived from septicidal capsules, are almost universal in Iridaceae. Septicidal capsules occur in most Melanthiales and Colchicaceae of Liliales and are probably basic for the order. Iridaceae may therefore be specialized in their possession of loculicidal capsules. The seeds of Liliiflorae have been extensively studied by Huber (1969), who found several features in the seeds of Iridaceae that distinguish generic groups. No seed characters have been used in this study as it seems likely that the basic seed type in the family is unspecialized and

TABLE 2. Embryological data known for Iridaceae. Abbreviations: su = successive; si = simultaneous; he = helobial; nu = nuclear. Unless specific references are given, the data are from Schnarf (1931).

	Micro-sporo-genesis	Parietal cell	Parietal tissue	Endo-sperm formation	References
ISOPHYSIDOIDEAE					
			Unknown		
NIVENIOIDEAE					
Geosiris aphylla	su	+	+	he	Goldblatt et al. (1987)
IRIDOIDEAE					
Iris tenax	–	+	+	nu	Smith & Clarkson (1956)
I. stylosa	–	+	+	–	
I. pseudacorus	–	–	–	nu	
I. fulva	–	+	–	–	Riley (1942)
I. hexagona subsp. *giganticaerulea*	–	+	–	–	Riley (1942)
Sisyrinchium striatum	si	+	x	nu	Lakshmanan & Phillip (1971)
S. californicum	si	+	x	nu	Lakshmanan & Phillip (1971)
Gelasine azurea	–	x	x	nu	Kenton & Rudall (1987)
Eleutherine latifolia	–	x	x	nu	Kenton & Rudall (1987)
IXIOIDEAE					
Crocus sieberi	–	–	–	nu	Rudall et al. (1984)
Romulea columnae	–	+	–	nu	
R. bulbocodium	–	+	–	nu	
R. rosea var. *reflexa*	–	+	x	nu	Steyn (1973a, b)
Tritonia crocata	–	–	–	nu	

In addition, simultaneous microsporogenesis has been reported in the following: *Sisyrinchium bushii* (Farr, 1922); *S. striatum*; *S. bermudiana*; *Crocosmia crocosmiiflora*; *C. aurea* (as *Tritonia*); *Chasmanthe aethiopica* (as *Antholyza*); *Gladiolus cunonius* (as *Antholyza*); *Ixia paniculata*; *I. coccinea*; *I. maculata*; and *Freesia refracta* (Guignard, 1915a); and *Tigridia pavonia*; *Crocus sativus*; *C. vernus*; *Gladiolus* ×*gandavensis* (Guignard, 1915b).

almost identical with that in several other families of Liliales, notably Colchicaceae and Campynemataceae. Huber did, however, record the presence of a lipid layer in the inner layer of the outer integument of the testa as a family characteristic (thus presumably a synapomorphy). Seed storage products include protein, oil, and hemicellulose, the latter present in the thick cell walls of the endosperm.

EMBRYOLOGY

Embryology of Iridaceae is poorly known (Table 2), so the generalizations made below for the family are tentative. Microsporogenesis, so far as is known, is reported to be simultaneous in the few genera of Iridoideae and Ixioideae examined: *Iris*, *Sisyrinchium*, *Tigridia*, *Crocus*, *Freesia*, *Romulea*, *Crocosmia*, *Ixia*, *Chasmanthe*, *Gladiolus*, incl. *Anomalesia* (Guignard, 1915a, b). Until recently no Nivenioideae nor *Isophysis* had been investigated embryologically, but Rübsamen (pers. comm.; Goldblatt et al., 1987) has found successive microsporogenesis in *Geosiris*. This suggests that the latter condition may be basic for Iridaceae, as it is for other families of Liliales and Melanthiales (Dahlgren & Bremer, 1985).

Unlike most Liliales, but typical of Melanthiales, the archesporial cell produces a parietal cell in most members of the family (*Iris*, *Romulea*, *Crocus*, *Crocosmia*, *Sisyrinchium*) and, except in *Sisyrinchium* where it degenerates, one or two layers of parietal tissue are formed (Wunderlich, 1959). In the two species of Tigridieae (*Gelasine* and *Eleutherine*) examined, the archesporial cell functions as the megaspore mother cell and the ovules are thus tenuinucellate. The embryo sac is of the *Polygonum*-type, basic for the monocots. Endosperm formation is nuclear (Wunderlich, 1959) in the few genera of Iridoideae (*Iris*, *Sisyrinchium*) and Ixioideae (*Romulea*, *Tritonia*) so far examined but helobial in *Geosiris* (Rübsamen, pers. comm.), the only species of Nivenioideae known in this

respect. By extension, helobial endosperm formation may be basic in Iridaceae if the condition is ancestral to nuclear endosperm formation, as some authorities believe (Dahlgren & Bremer, 1985). Embryological data are urgently needed for more genera of Nivenioideae and for *Isophysis*. In Melanthaceae endosperm formation is also helobial.

CYTOLOGY

Chromosome number, size, and morphology are variable in Iridaceae, and the basic number for the family is uncertain, particularly as *Isophysis* is unknown cytologically (Goldblatt, 1971, 1979a, 1982b; Kenton & Heywood, 1984). The most likely basic number for Nivenioideae, Iridoideae, and Ixioideae is $x = 10$, judging from the distribution of base numbers in the less specialized genera. A derived basic number is known for Tigridieae, which are unusually uniform cytologically and have $x = 7$ (Goldblatt, 1982b). The closely related Mariceae probably have $x = 10$. The base number of $x = 7$ may reasonably be treated as an autapomorphy for Tigridieae even though base numbers for other tribes are not certain. Irideae also possibly have $x = 10$, but the situation in *Iris* and its immediate allies is so complex that this is very speculative and 10 is in any event possibly basic for the family. For each tribe of Ixioideae the most likely base number is also $x = 10$.

ANATOMY

Several aspects of the anatomy of Iridaceae have recently been examined by Rudall (1983, 1984, 1986), and as a result a number of anatomical features can be used with some confidence for phylogenetic analysis. The primary thickening meristem (PTM) is characteristically well developed in the rhizomes of *Isophysis*, *Aristea*, and *Patersonia* (Nivenioideae) and *Orthrosanthus* and *Libertia* (Sisyrinchieae); consequently these genera have rhizomes with substantial pericyclic vasculature and usually a prominent endodermis. Irideae and Mariceae have a reduced PTM and little pericyclic vasculature. The endodermis thickening is reduced in many Irideae and absent in Mariceae. Similar reduction is characteristic of the corms of Ixioideae. The latter, excepting *Pillansia*, have a distinctive leaf epidermis, regarded as derived here, in which the cells have sinuous walls and two or more papillae. The mesophyll in many Ixioideae, but not *Pillansia*, is also modified in being elongated along the horizontal axis of the leaf (Rudall, pers. comm.).

Secondary growth occurs in most Nivenioideae. *Klattia*, *Witsenia*, and *Nivenia* are woody shrubs while *Patersonia* has woody underground stems (Rudall, 1986). The apparently less specialized *Aristea* and *Geosiris*, however, do not have secondary growth and the condition is unlikely to be a synapomorphy for the tribe as a whole. Secondary growth may have evolved only once in the subfamily, for *Patersonia* shares with the shrubby Cape genera several specializations in leaf anatomy and similar flavonoid characters not present in *Aristea* (Rudall & Burns, 1989).

Leaf margins also provide characteristics that seem significant. These include subepidermal sclerenchyma, a synapomorphy for Irideae and for *Isophysis*. Subepidermal marginal sclerenchyma is an important xeromorphic feature and the condition is developed independently in several genera. In many Ixioideae the subepidermal marginal sclerenchyma is associated with a vein, which will be useful later in defining natural generic groupings and phylogeny in the large and diverse Ixieae, not attempted in this paper. Mariceae have marginal epidermal cells heavily thickened and radially elongated but lack subepidermal sclerenchyma (Rudall, pers. comm.). A similar epidermis occurs in a few genera of Ixieae, in which it may have evolved more than once. The presence of a distinct leaf midrib is most likely a derived condition in Iridaceae and is present in all Watsonieae and Ixieae (Ixioideae) but not in Pillansieae. In Iridoideae, Mariceae also have leaf midribs, but the related Tigridieae have plicate leaves with more than one major vein, this probably directed related to the foliated nature of the leaf. Most genera of Irideae and Sisyrinchieae lack leaf midribs.

It has been known for several years that vessels are confined to the roots of Iridaceae except *Sisyrinchium* (Cheadle, 1963). The vessel perforations are scalariform (the plesiomorphic condition) in *Isophysis* and Nivenioideae (including *Geosiris*) (Goldblatt et al., 1987). Elsewhere in the family the vessel perforations are simple or predominantly simple (Cheadle, 1963). This is regarded as a synapomorphy for Iridoideae and Ixioideae and is apparently a major synapomorphy (Fig. 3) uniting the two subfamilies. Vessels are present in the stems and leaves of *Sisyrinchium*. Too few species and genera of Sisyrinchieae have been examined for vessels, and their presence in the stems and leaves may be extended to the closer allies of *Sisyrinchium*. However, *Libertia*, *Orthrosanthus*, and *Bobartia* of the tribe have vessels only in the roots.

Styloid calcium oxalate crystals are a family characteristic (Goldblatt et al., 1984) for Iridaceae. Long styloids are found in most tissues of all genera,

especially in the vascular bundles. Styloids are, however, lacking in *Sisyrinchium* (Goldblatt et al., 1990) and its close relatives (e.g., *Olsynium, Solenomelus*). In Liliales no other family has styloids, but this type of crystal occurs in several genera of Melanthiaceae (tribes Melanthieae and Narthecieae) where they are confined to the vascular sheaths (Ambrose, 1980). Several genera of these tribes have, in addition, raphide bundles in parenchyma tissue. The polarization of the styloid character for Iridaceae largely depends on what family is regarded as the immediate ancestor or sister group of Iridaceae. Styloids, reported previously as lacking in *Geosiris* (from the scalelike leaves) by Goldblatt et al. (1984), have now been found in the stems and rhizomes of the genus (Goldblatt et al., 1987), and this is taken as important evidence for the placement of *Geosiris* in Iridaceae.

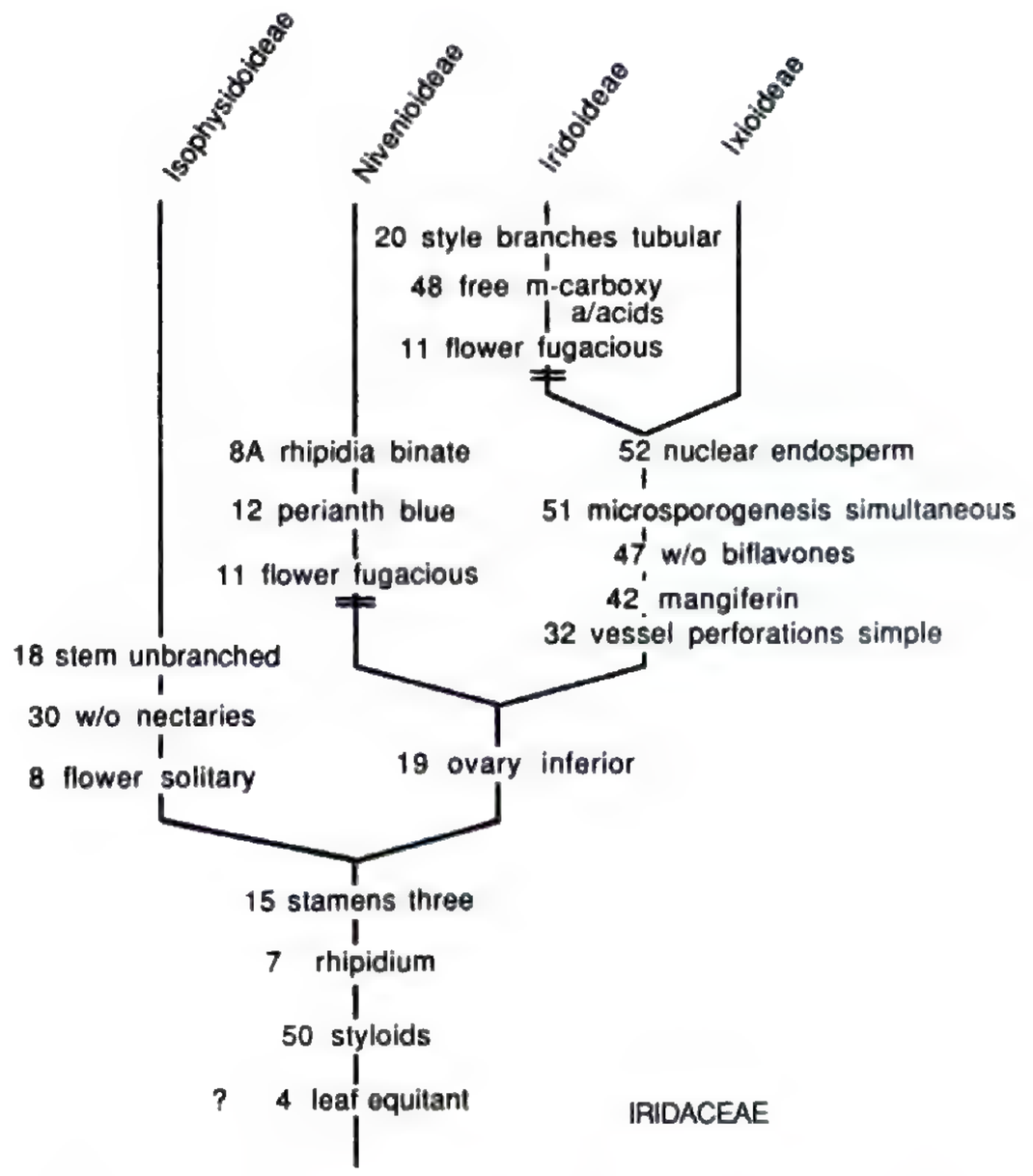

FIGURE 3. Cladogram of the major lineages of Iridaceae, here treated as subfamilies. Parallelisms are indicated by double lines. The characters are polarized assuming Iridaceae belong to Liliales. See Table 1 for explanation of characters used here.

PHYTOCHEMISTRY

Flavonoids. Iridaceae have an unusually wide range of flavonoid compounds compared with other petaloid monocot families (Williams et al., 1986). Basic to the Liliiflorae are most likely *O*-glycosides of the flavonols quercetin and kaempferol (Williams, 1975), and perhaps flavone *C*-glycosides, the latter of wide distribution in the monocots although rare in Liliiflorae apart from Iridaceae and Orchidaceae. Basic for Iridaceae are flavonol *O*-glycosides and flavone *C*-glycosides, as well as biflavones. The last-mentioned are unusual in the flowering plants but have now been recorded in a few Liliiflorae: *Isophysis* and *Patersonia* in the Iridaceae and an unconfirmed report in *Lophiola* (Melanthiaceae). The distribution of biflavones in the petaloid monocots is inadequately known at present, but it seems likely that their presence may be basic for Liliiflorae as a whole rather than a specialization in Iridaceae. If plesiomorphic, they have been lost in Iridoideae and Ixioideae. The possible biflavones provisionally identified in Iridoideae are probably *C*-methylated flavonoids (C. Williams, pers. comm.).

Important flavonoid features for phylogenetic consideration (data from Williams et al., 1986) include the absence of flavone *C*-glycosides in Pillansieae and Watsonieae (both Ixioideae) (provisionally regarded as apomorphic states for these tribes) and the accumulation of flavones (apparently an important synapomorphy) and flavone *O*-glycosides in Ixieae. *Pillansia* has a flavonol sulfate, unique in Iridaceae. Nivenioideae appear unusual in having a predominance of flavonol *O*-glycosides, including unusual myricetin derivatives and only traces of or no flavone *C*-glycosides. Sisyrinchieae, Mariceae, and Tigridieae stand out in largely or entirely lacking flavonols. A significant synapomorphy for Iridoideae and Ixioideae appears to be the frequent, but not universal, accumulation of the xanthone *C*-glycoside mangiferin.

Free amino acids and peptides. The unusual free amino acids carboxyphenylalanine and caboxyphenylglycine have a distinctive distribution in Iridaceae (Larsen et al., 1981), occurring regularly in most species examined of Iridoideae, but these compounds are notably absent from *Sisyrinchium* (its immediate allies have not been surveyed), yet recorded in *Libertia, Bobartia,* and *Orthrosanthus,* also Sisyrinchieae. The presence of these distinctive amino acids, not reported elsewhere in the monocotyledons, is regarded as a major synapomorphy for Iridoideae, united otherwise by having a fugacious flower (a parallelism with Nivenioideae) and convolute style branches.

A second unusual group of compounds, γ-glutamyl peptides, have been found to be common in Irideae, and also present in about half the species of Mariceae examined. They have not been reported in Tigridieae, in which only three species have been surveyed. Gamma-glutamyl peptides are absent in all Ixioideae and Nivenioideae (known for

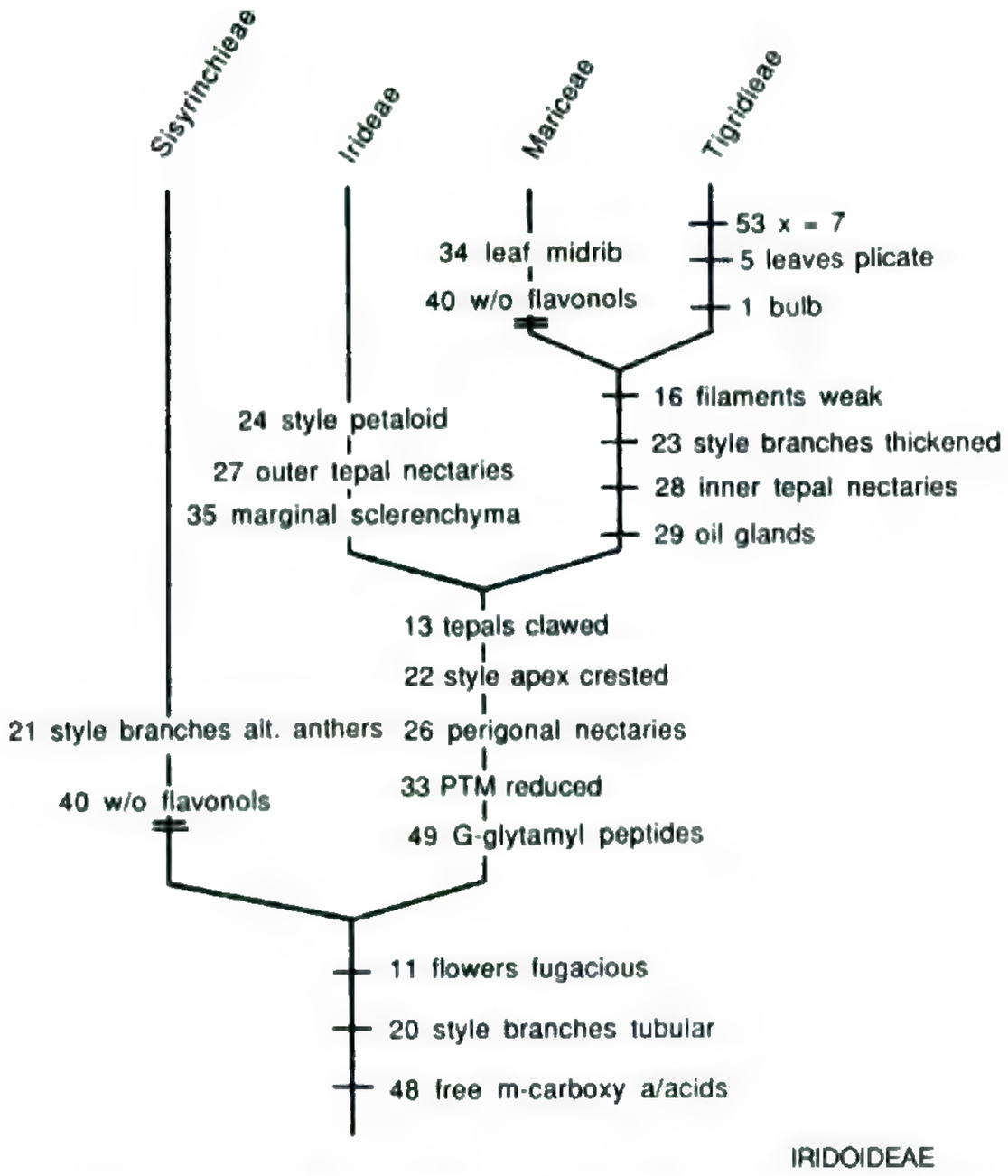

FIGURE 4. Cladogram of subfamily Iridoideae with the major lineages treated as tribes. Parallelisms are indicated by double lines. See Table 1 for explanation of characters used.

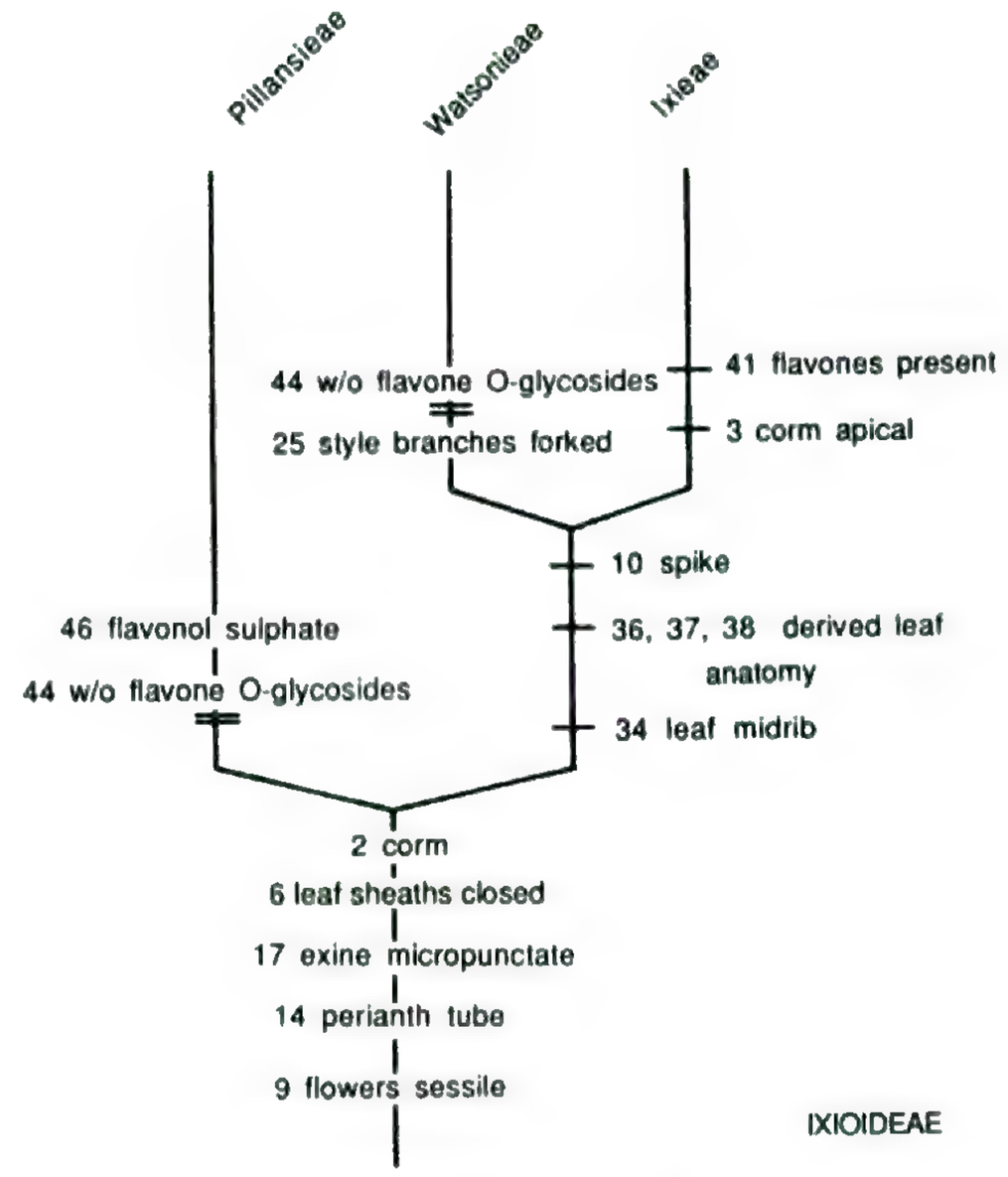

FIGURE 5. Cladogram of subfamily Ixioideae with lineages treated as tribes. Parallelisms are indicated by double lines. See Table 1 for explanation of characters.

only two species of the latter) examined (Larsen et al., 1981, 1987). The presence of this class of compounds is treated as a synapomorphy for the line including Irideae, Mariceae, and Tigridieae. It seems likely that γ-glutamyl peptides will be found in Tigridieae when more species are surveyed, and their absence cannot at present be regarded as a reversal for the tribe. These peptides are not invariably present in Irideae, and are sometimes absent in some species in a genus in which they have been found, or even lacking in some genera. Further sampling is needed.

CLADISTIC ANALYSIS

The results of the cladistic analysis are presented in three diagrams (Figs. 3–5), the first for the major lineages of Iridaceae, and the second and third for the large subfamilies Iridoideae and Ixioideae. The manually generated cladograms were tested using the PAUP Program (Swofford, 1985), which produced the same results. There is good evidence that Iridaceae are monophyletic and defined by several synapomorphies, the number depending on the chosen outgroup, which for this study is the Melanthiales. There are four major lineages (Fig. 3), one for *Isophysis* alone, and the other three united by the possession of an inferior ovary. These four primary lineages are accorded subfamily rank.

Ixioideae are distinguished by five important apomorphic states. Iridoideae and Ixioideae share five synapomorphies. The xanthone, mangiferin, occurs in many genera of both subfamilies, and specialized vessels with simple perforations have been found in all genera so far examined. This clade also lacks biflavones and is specialized embryologically in having simultaneous microsporogenesis and nuclear endosperm formation, although too few genera have been studied embryologically. Biflavones are basic in Iridaceae but absent in Ixioideae and probably absent in Iridoideae since the unidentified DK/DK compounds suggested to be biflavonoids in a few Iridoideae (Williams et al., 1986) are most likely *C*-methylated flavonoids (Williams, pers. comm.). Nivenioideae are united by having compound rhipidia (usually binate). Their derived fugacious flowers with blue perianths appear to be basic for the subfamily.

The cladogram for Iridoideae (Fig. 4) also has four major lines, accorded tribal status, and corresponding closely to currently accepted tribal groups in the family. The status and composition of Sisyrinchieae, however, is still open to question. The core genera of the tribe, around *Sisyrinchium* and its close allies in South America, are clearly monophyletic, but it is not yet established with any confidence that the southern African *Bobartia*, or the Australasian–South American *Libertia* and *Orthosanthus* also belong here. Their present position

rests to some extent on inadequately investigated phytochemical data and on a subjective interpretation of the nature of style branch structure and orientation.

In Ixioideae there seem to be three distinct lines (Fig. 5) and each is accorded tribal rank. The monotypic Pillansieae are isolated from the line leading to Watsonieae and Ixieae and are clearly ancient and primitive relicts. Watsonieae and Ixieae are less well defined but nevertheless appear to comprise natural groups of equal rank. Ixieae comprise almost half the genera and species of the family and it would be most satisfactory if this tribe could be broken down into a few large groupings. However, at present this does not seem possible, although some 6–8 small generic groupings (see discussion below under Radiation and Composition of the Subfamilies—Ixioideae) are apparent.

Radiation and Composition of the Subfamilies

ISOPHYSIDOIDEAE

Consisting only of the Tasmanian *Isophysis* (Fig. 1A), the subfamily is typical of Iridaceae in lacking the three stamens of the inner whorl, and in having styloid crystals (Goldblatt et al., 1984), extrorse anthers, and distichously arranged equitant leaves. It differs markedly, however, in having a superior ovary, which isolates *Isophysis* from the rest of the family. It is also somewhat discordant in its flavonoids: apart from traces of flavone *C*-glycosides, it has biflavones only (Williams et al., 1986), compounds also found in some Nivenioideae. The basic inflorescence of *Isophysis* is interpreted here as a rhipidium. It consists of a single terminal flower, but its arrangement in two large opposed spathelike bracts that enclose the bud and pedicel is very like that of the rhipidium that is probably basic in Iridaceae. *Isophysis* apparently lacks nectaries (Cooke, 1986).

NIVENIOIDEAE

Including one Australasian and five Afro-Madagascan genera, the largest of which is the widespread *Aristea* (ca. 50 spp.), Nivenioideae comprise some 83 species. *Nivenia*, *Witsenia*, and *Klattia*, all shrubby (Fig. 1B) and with strongly developed secondary growth of the monocot type, are endemic to the southwestern Cape. *Geosiris*, an achlorophyllous saprophyte with scalelike leaves, is restricted to moist forests in eastern Madagascar. It has numerous ovules and fine seeds but in other respects appears to conform with Nivenioideae (Goldblatt et al., 1987). Most notable are the styloid crystals in the stems and in the cormlike rhizomes, and the vessels with scalariform perforations (the basic condition in Iridaceae), and found in *Isophysis* and the genera of Nivenioideae. The non-African genus, *Patersonia*, is mainly Australian (Cooke, 1986) and occurs on New Guinea, Sumatra, and Borneo.

Nivenioideae are specialized in their fugacious and blue flowers (almost certainly derived in the family), either binate or variously fused rhipidia, and unusual flavonoid pattern with a predominance of flavonol *O*-glycosides rather than flavone *C*-glycosides, which are more common elsewhere in Iridaceae. *Aristea* exhibits little specialization except in capsule and seed morphology. The shrubby Cape genera all have flowers with a well-developed perianth tube, a derived condition. *Witsenia* is specialized for sunbird pollination and has yellow, green, and black flowers. *Nivenia* is unusual in its heterostyly, probably basic in the genus and found in five of the nine species.

Patersonia has a specialized floral morphology: the tepals are united in a long slender tube, the inner tepals are reduced to scales or are absent, and the stigma lobes are more or less fringed. The roots are woody and have secondary growth (Rudall, 1986). Woodiness in *Patersonia* and the shrubby Cape genera may have had a common origin, as these genera share a similar leaf anatomy and flavonoid profile (Rudall & Burns, 1989). However, the Cape genera share with *Aristea* the derived basic chromosome number, $x = 16$ (Goldblatt, 1971), while *Patersonia* may have $x = 11$ (Goldblatt, 1979a).

IRIDOIDEAE

Iridoideae share with Ixioideae vessels with specialized simple perforations and the arguably significant phytochemical character of having, in at least a few species of each, the xanthone mangiferin, an unusual compound in the monocots. All genera of both subfamilies also lack biflavones. Possibly these three features arose independently in each subfamily, and certainly they appear to share no significant morphological specializations while differing in a large number of features. Iridoideae are united by having fugacious flowers (a parallelism with Nivenioideae), perigonal nectaries, and an unusual style morphology in which the branches are long and divide below the level of the anthers while the margins are conduplicate so that each branch is stigmatic only apically. This style

TABLE 3. Classification of the Iridaceae, with the genera assigned to subfamily and tribe. Numbers in parentheses indicate the total genera and species for tribe or subfamily or total species for a genus. Important synonyms are indicated. Total 77 genera, 1,630 species.

1. Subfamily Isophysidoideae Takhtajan (1980) (1 : 1)
   Isophysis (1)—Tasmania
2. Subfamily Nivenioideae Schulze (1971) ex Goldbl.[1] (6 : 83)
   Aristea (50)—Africa, Madagascar
   Geosiris (1)—Madagascar
   Nivenia (9)—Cape Region, South Africa
   Klattia (2)—Cape Region, South Africa
   Witsenia (1)—Cape Region, South Africa
   Patersonia (20)—Australia, Borneo, Sumatra, New Guinea
3. Subfamily Iridoideae (42 : 690)
   Tribe Sisyrinchieae Baker (1878) (8 : 124)
   Bobartia (12)—southern Africa
   Libertia (ca. 9)—Australasia, South America
   Diplarrhena (2)—southeastern Australia, Tasmania
   Orthrosanthus (9)—Australia, South and Central America
   Sisyrinchium (ca. 80)—North and South America
   Olsynium (incl. *Phaiophleps*, *Chamelum*, *Ona*) (11)—North and South America
   Solenomelus (2)—Chile, Argentina
   Tapeinia (1)—southern Chile and Argentina
   Tribe Irideae (13 : 405)
   Dietes (6)—East and southern Africa, Lord Howe Island
   Moraea (120)—sub-Saharan Africa
   Homeria (incl. *Sessilistigma*) (32)—southern Africa
   Rheome (3)–western Cape, South Africa
   Hexaglottis (6)—western Cape, South Africa
   Roggeveldia (1)—Karoo, South Africa
   Barnardiella (1)—western Cape, South Africa
   Gynandriris (9)—southern Africa, Mediterranean, Middle East
   Galaxia (14)—South Africa
   Pardanthopsis (1–2)—eastern Asia
   Belamcanda (1)—southeastern Asia
   Iris (ca. 210)—Europe, Asia, North Africa, North America
   Hermodactylis (1)—Mediterranean Middle East
   Tribe Mariceae Hutchinson (1934) (3 : 40)
   Trimezia (ca. 20)—South and Central America
   Pseudotrimezia (6–8)—Brazil
   Neomarica (ca. 12)—South and Central America
   Tribe Tigridieae Baker (1878) (18 : 125)
   Cypella (ca. 20)—South and Central America
   Cipura (ca. 6)—South and Central America, West Indies
   Eleutherine (2)—South and Central America, West Indies
   Ennealophus (5)—South America
   Gelasine (4)—South America
   Calydorea (incl. *Cardiostigma*, *Catila*, *Itysa*) (ca. 10)—temperate South America
   Ainea (2)—Mexico
   Nemastylis (5)—Central America, Mexico, southern U.S.A.
   Herbertia (ca. 6)—temperate South America, southern U.S.A.
   Onira (1)—temperate South America
   Kelissa (1)—temperate South America
   Mastigostyla (ca. 16)—South America
   Cardenanthus (ca. 8)—South America
   Tigridia (ca. 35)—South and Central America
   Sessilanthera (3)—Mexico and Central America
   Alophia (ca. 5)—tropical South and Central America, southern U.S.A.
   Fosteria (1)—Mexico
   Cobana (2)—Guatemala, Honduras

TABLE 3. Continued.

4. Subfamily Ixioideae Klatt (1866) (as subordo Ixieae) (28 : 860)
   Tribe Pillansieae Goldblatt[2] (1 : 1)
   Pillansia (1)—southwestern Cape, South Africa
   Tribe Watsonieae Klatt (1882) (5 : 99)
   Lapeirousia (ca. 36)—tropical and southern Africa
   Savannosiphon (1)—south tropical Africa
   Micranthus (3)—southwestern Cape, South Africa
   Thereianthus (7)—southwestern Cape, South Africa
   Watsonia (52)—southern Africa
   Tribe Ixieae Dumortier (1822) (22 : 760)
   Ixia (45)—South Africa
   Dierama (44)—tropical and southern Africa
   Sparaxis (including *Synnotia*) (12)—southwestern Cape, South Africa
   Freesia (11)—southern Africa
   Anomatheca (6)—south tropical and southern Africa
   Crocosmia (9)—south tropical and southern Africa
   Devia (1)—southern Africa
   Chasmanthe (3)—southwestern Cape, South Africa
   Tritonia (28)—south tropical and southern Africa
   Duthieastrum (1)—southern Africa
   Geissorhiza (82)—South Africa
   Hesperantha (ca. 62)—tropical and southern Africa
   Schizostylis (1)—southern Africa
   Melasphaerula (1)—southern Africa
   Gladiolus (incl. *Homoglossum*, *Anomalesia*, *Oenostachys*) (ca. 195)—Africa, Madagascar, Eurasia
   Radinosiphon (1–2)—south tropical and southern Africa
   Babiana (incl. *Antholyza*) (64)—southern Africa, Socotra
   Tritonopsis (incl. *Anapalina*) (22)—South Africa
   Zygotritonia (4)—tropical Africa
   Romulea (ca. 90)—Africa, Mediterranean
   Syringodea (8)—southern Africa
   Crocus (ca. 80)—Europe, Asia, North Africa

[1] **Nivenioideae** Schulze ex Goldblatt, subfam. nov. Plantae foliis sine costis medianis, caulibus subterraneis vel aeriis et saepe lignosis, inflorescentiis binatis, floribus actinomorphis usitate caeruleis, tepalis plus minus liberis vel in tubum connatis.

[2] **Pillansieae** Goldblatt, trib. nov. Planta foliis sine costis medianis, inflorescentia paniculata, floribus sessilibus actinomorphis, tepalis in tubum connatis, stigmatibus plus minus integribus.

type seems basic to the subfamily but is variously modified in specialized lines. Another significant specialization in Iridoideae is the presence of the free amino acids meta-carboxyphenylalanine and glycine (Larsen et al., 1981, 1987).

Iridoideae comprise four important lines, which are treated here as tribes. The least specialized of these is the Sisyrincheae (Fig. 2A, B). The tribe may be heterogeneous, and an absence of apomorphic features makes it difficult to deal with. Possibly it is united by having the long style branches extending between the stamens rather than opposite them (this feature may be basic for the subfamily). All the species so far examined for flavonoids are apparently derived in not accumulating flavonols (a reversal). *Libertia* and *Orthrosanthus* occur in Australasia and South America, the latter also in Central America, while *Diplarrhena* is restricted to southeastern Australia and Tasmania. The large and diverse *Sisyrinchium* and its close allies, including *Olsynium* (incl. *Phaiophleps* and *Ona*), *Tapeinia*, and *Solenomelus*, all small genera, are solely New World and centered in South America. *Bobartia* appears unusual phytogeographically in being southern African (Strid, 1972).

The floral morphology of *Bobartia* is virtually identical with other Sisyrinchieae but it has two unusual features: pubescent pedicels and scattered fibers in the phloem (Rudall, 1983). The latter is a constant attribute of several African genera of Irideae, including *Dietes* and *Moraea*, while pubescent pedicels are known elsewhere in Iridaceae only in *Dietes*. If *Bobartia* is misplaced in Sisyrinchieae, it may have acquired its apparently simple floral morphology by a reversal to a more

FIGURE 6. Iridoideae tribe Irideae.—A. *Moraea atropunctata* Goldbl., habit and detail of the stamens and gynoecium.—B. Corm of *Moraea* with tunics removed showing apical origin of roots.—C. *Iris afghanica* Wendelbo, habit (from Hedge & Wendelbo, 1972—@ Crown copyright. Reproduced with the permission of the Controller of her Britannic Majesty's Stationery Office).—D. *Hexaglottis namaquana* Goldbl., habit, flower, and detail of the stamens and gynoecium.—E. *Galaxia luteo-alba* Goldbl., showing acaulescent habit. Habits ×½, details life-size or variously enlarged.

primitive condition, such as is likely to have occurred in *Eleutherine*—Tigridieae and *Roggeveldia*—Irideae, for example (Goldblatt, 1979b). Alternatively, the tribes as delimited here require reevaluation. The flavonoids and other phytochemical features of *Bobartia* are poorly sampled and further investigation may resolve the conflict.

The three other important assemblages in Iridoideae form a clade united by having flowers in which the tepals are differentiated into a limb and claw, and in which the upper apices of the style branches are produced into nonstigmatic paired appendages (crests). The unusual γ-glutamyl peptides are present in most members examined (but notably not yet reported in Tigridieae, of which only four species have been sampled). Irideae, centered in the Old World, have the style branches and crests flattened and petaloid (Fig. 6A), nectaries restricted to the base of the outer tepals (at least in the less specialized genera), and, in all genera, a characteristic subepidermal marginal sclerenchyma. The largest genus is *Iris*, mainly Eurasian but also in North America, and often treated as several genera (Rodionenko, 1961), including *Iridodictyum*, *Xiphium*, and *Scorpiris*, all of which have bulbs, and *Junopsis*, which has swollen roots and a vestigial rootstock. The phylogeny of *Iris* s.l. needs careful study before the several segregates are finally accepted. In sub-Saharan Africa there are *Dietes*, with one species on Lord Howe Island, and several genera with apically rooting corms, notably *Ferraria*, *Moraea*, *Homeria*, and *Galaxia*. All but *Ferraria* also have a secondarily bifacial dorsiventral leaf. *Moraea*, the largest genus with some 120 species, has radiated extensively in southern and east tropical Africa (Goldblatt, 1977, 1986a). The other genera, all apparently segregates of *Moraea* (Goldblatt, 1987 and in prep.), are centered in the winter rainfall area of the southwestern coast of southern Africa.

Three subtribes have been proposed for Irideae (Goldblatt, 1976): Iridinae (*Iris*, *Belamcanda*, *Hermodactylis*, and *Pardanthopsis*); Ferrariinae (*Ferraria*); and Homeriinae (*Moraea*, *Homeria*, *Galaxia*, *Hexaglottis*, *Gynandriris*, and other genera). The disposition of *Dietes* is somewhat uncertain although in the past I have aligned it with Iridinae (Goldblatt, 1981).

In the New World, Mariceae and Tigridieae share an apparently identical flower with thickened style branches (in contrast to the flattened branches of Irideae), nectaries best developed on the inner tepals, and unusual slender and weak filaments so that the anthers are supported by being attached to the style branches. The nectaries also produce oils (Vogel, 1974) secreted by clavate elaiophores.

FIGURE 7. Ixioideae. *Pillansia templemannii* L. Bolus. Inflorescence ×½, rootstock and leaf ×⅛.

Mariceae, comprising *Trimezia*, *Neomarica*, and possibly *Pseudotrimezia*, have leaves with distinct midribs and they apparently lack flavonols (a parallelism with Sisyrinchieae). Tigridieae, a larger tribe, are poorly understood taxonomically. They have three important synapomorphies: plicate leaves, a distinctive type of bulb, and the derived basic chromosome number of $x = 7$. Tigridieae have radiated extensively in temperate and Andean South America, and in Mexico. Major specializations are all floral and focus on the style and sta-

FIGURE 8. Ixioideae.—A. *Watsonia spectabilis* L. Bolus, habit.—B. Detail of corm of A with tunics removed showing basal origin of the roots.—C. *Hesperantha luticola* Goldbl., habit and flower.—D. *Geissorhiza mathewsii* L. Bolus, habit and detail of flower and leaf section.—E. *Lapeirousia lewisiae* B. Nord., habit and flower. Habits ×½, details life-size or variously enlarged.

mens. Several new and mostly monotypic genera have recently been described by Ravenna (1981, 1983, 1986), and it seems clear that the current systematics, based on the minor variations in the shape or disposition of the style branches and the degree of fusion of the filaments, is unsatisfactory and is leading to the chaotic proliferation of monotypes. Careful cladistic analysis may point the way to a more acceptable taxonomy, reflecting as far as possible, natural relationships.

Two subtribes have been proposed in Tigridieae (Goldblatt, 1982b), Cipurinae, with a base number of $x = 7$, monosulcate pollen grains, and generally simple, thickened style branches, and Tigridiinae, with x usually = 14, bisulcate pollen grains, style branches deeply divided into filiform arms, and stamens united.

IXIOIDEAE

Ixioideae (Figs. 7, 8) are remarkably distinct from other Iridaceae in numerous features. The subfamily is centered in southern Africa, with the specialized genera *Romulea* and *Gladiolus* also in Eurasia, where the large genus *Crocus* has radiated. Synapomorphies for Ixioideae (Fig. 5, Table 1) are presence of perianth tubes, basal rooting corms, inflorescences of sessile flowers arranged in a panicle or spike (Fig. 8), micropunctate pollen exines, and closed leaf sheaths. All Ixioideae so far examined have septal nectaries (Daumann, 1970), which may be the basic condition in the family.

Ixioideae comprise over 860 species, about half the family, and some 760 of these belong in Ixieae. The monotypic Cape *Pillansia* is taxonomically isolated in the subfamily, and is the only genus with a panicle (Fig. 7), presumably ancestral to the spike, which is basic to the other two tribes. These also have distinct leaf midribs and specialized leaf anatomy (Rudall, pers. comm., see earlier discussion of leaf anatomy). *Pillansia* also lacks flavone *C*-glycosides (a parallelism with Watsonieae). This genus is apparently unique in Iridaceae in having a flavonol sulfate. Despite the undesirability of monotypic groups, it seems necessary to treat *Pillansia* as the only member of a tribe Pillansieae.

Watsonieae comprise some 99 species in 5 genera, which share unusual deeply divided style branches as well as the absence of flavone *C*-glycosides (as does *Pillansia*). The tribe includes the southern African *Watsonia*; two endemic Cape genera, *Thereianthus* and *Micranthus*; *Lapeirousia*, spread through sub-Saharan Africa; and the monotypic south tropical African *Savannosiphon*. *Watsonia* is extremely variable in its floral morphology, and bird-pollinated flowers (e.g., Fig. 8A) have evolved independently in at least three lines in the genus (Goldblatt, 1989).

Ixieae have corms that develop partially from the apical bud (explained in detail earlier), an unusual array of flavones not found in the rest of the family, and flavone *O*-glycosides. Some eight subtribes have been recognized in Ixieae as here circumscribed (Lewis, 1954; Goldblatt, 1971), all relatively small monophyletic assemblages, each of which has a common basic chromosome number and unique character combination. These subtribes include Ixiinae (*Ixia*, *Dierama*, *Sparaxis*), x = 10, membranous and usually dry bracts, filiform style branches, and fibrous corm tunics; Tritoniinae (*Tritonia*, *Crocosmia*, *Chasmanthe*, *Duthieastrum*), $x = 11$, short subherbaceous bracts, orange flower colors, and fibrous corm tunics; Gladiolinae (*Gladiolus* including *Homoglossum*, *Anomalesia*, and *Oenostachys*; *Radinosiphon*), $x = 15$, long herbaceous bracts, wiry corm tunics, spathulate style branches, and winged seeds; Hesperanthinae (*Geissorhiza*, *Hesperantha*, *Schizostylis*, and possibly *Melasphaerula*), $x = 13$, more or less herbaceous bracts, woody corm tunics, filiform style branches; Babianinae (only *Babiana*, $x = 7$, subfibrous tunics, plicate leaves, spathulate style branches, and herbaceous bracts; Romuleinae (*Crocus*, *Romulea*, *Syringodea*), possibly $x = 13$, woody corm tunics, flowers solitary on the branches of the flowering stems, often divided style branches. Additionally, *Freesia* and *Anomatheca*, both x = 11, and *Tritoniopsis*, apparently $x = 16$, are allied and have been placed in Freesiinae and Anapalinae respectively. Their affinities to other genera of Ixieae are uncertain, but similarities in leaf margin epidermis (Rudall & Goldblatt, in press) suggest links with Tritoniiae. The relationships of the tropical African *Zygotritonia* are likewise uncertain.

There are probably several old and taxonomically isolated lines in Ixieae. However, genera within each line are often not well defined and may be of comparatively recent origin. Zygomorphic flowers have evolved independently in most lines (Fig. 8A, E), sometimes, as in *Geissorhiza*, *Babiana*, and *Gladiolus*, more than once in each. Large bird-pollinated flowers with red to orange perianths, long dimorphic tubes, and exserted anthers and style branches have also evolved independently in at least three lines with *Gladiolus* (Goldblatt & de Vos, 1989), in *Babiana* (*B. ringens*), *Chasmanthe*, and *Tritoniopsis*, as well as in *Watsonia* (Watsonieae). Convergence in floral form has obscured the natural relationships of many Ixioideae (Lewis, 1954), and vegetative morphology and chromosome cytology (Goldblatt, 1971) are now

accepted as more important for phylogenetic considerations above the species level than most floral features.

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EVOLUTION AND PHYLOGENY OF THE ARACEAE[1]

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Abstract

The Araceae are exceptionally diverse by nearly all phenetic criteria. The two most widely accepted infrafamilial classification systems, those of Engler and Hutchinson, emphasize vegetative and floral morphology, respectively, and are thus rather dissimilar. A more balanced scheme, in which all available phenetic data are considered, is attempted here. Character state polarities are inferred, and synapomorphies utilized to circumscribe infrafamilial taxa. Among the character states considered primitive for Araceae are: a rhizomatous or caulescent growth habit; simple, cordate leaf blades; parallel venation; a simple, green spathe; bisexual, perigoniate flowers; trilocular ovaries with axile placentation; anatropous, crassinucellate ovules; elongate stamens with longitudinal anther dehiscence; a base chromosome number of $x = 7$ or 14; and monosulcate, reticulate, binucleate pollen grains lacking starch. These and other conclusions have been employed in a character analysis of araceous subtaxa accepted a priori as natural. Significant features of the classification derived from a cladogram reflecting this analysis include: the merger of Engler's subfamilies Pothoideae and Monsteroideae, and the dissolution of his Calloideae; a drastic internal rearrangement of the Colocasioideae; and the recharacterization of the Aroideae, involving the transfer of several tribes to the Philodendroideae and the assimilation of the subfamily Pistioideae (*Pistia stratiotes* L.) and the tribe Thomsonieae (formerly included in subfamily Lasioideae). The following suprageneric nomenclatural novelties are created: Cercestideae Grayum, trib. nov.; Protarinae (Engl.) Grayum, stat. nov.; Remusatiinae Grayum, subtrib. nov.; Jasarinae Grayum, subtrib. nov.; and Scaphispathinae Grayum, subtrib. nov.

The Araceae, or aroid family, comprise about 107 genera and 2,500 species of monocotyledonous herbs and vines. Epiphytes and climbers account for approximately 70% of the total species (French, in press). Although the family occurs naturally in every continent except Antarctica, it is predominantly tropical: only about 10 genera extend into northern temperate zones (see Table 1), and no species occur in truly temperate regions of the Southern Hemisphere. Most aroid genera occur in tropical Asia and the New World tropics. Although Asia boasts a few more genera, the Neotropics are perhaps 50% richer in species (Croat, 1979). Roughly half of the species in the family are contained in just two of the 107 genera, *Anthurium* and *Philodendron*, both of which are exclusively neotropical. About 20 genera occur naturally in tropical Africa, though many of these are isolated and aberrant.

The Araceae are exceptionally diverse by nearly all phenetic criteria, as will be abundantly detailed in the present paper, and the family is certainly a comparatively old one. Nonetheless, it is apparently a natural and monophyletic group, as far as can be concluded from presently available evidence. This statement requires a footnote, however: the temperate, oligotypic genus *Acorus*, traditionally included in Araceae, is strongly discordant within this family; its inclusion seriously weakens the circumscription of the family and probably even renders the Araceae diphyletic. Grayum (1984, 1987) and Tillich (1985) have detailed the reasons for removing *Acorus* to its own family, Acoraceae, which Walker (manuscript) further isolated in its own infraclass, Acoriflorae (envisioned by Walker as a sister group to Ariflorae and Typhiflorae). Recent studies of restriction site variation in chloroplast DNA support separate family status for *Acorus* (French & Kessler, 1989). It has thus become clear that *Acorus* is extralimital to Araceae, hence the genus will not be dealt with further in the present paper.

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Minus *Acorus*, the family Araceae may be characterized by the following suite of probable synapomorphies (Grayum, 1984, 1987): a bractless, spicate inflorescence; extrorse anther dehiscence; a unipistillate gynoecium; a berrylike fruit; amoeboid anther tapetum; helobial (i.e., haustorial) endosperm development; and the (probably) universal presence of tannins. To this list may be added the following features which, though presumably plesiomorphic, help characterize the family: bifacial leaves; presence of raphides; lack of ethereal oil cells; hypogynous, actinomorphic flowers; basifixed anthers; successive pollen mother-cell cytokinesis; absence of perisperm; absence of silica; and absence of tricin. All of the above characteristics are universally present, as far as is known, in all genera of Araceae; furthermore, no other monocot taxon possesses them all in combination.

As regards most other characters, however, the Araceae are far from uniform, presenting a broad and in some cases (e.g., pollen exine sculpturing) all but bewildering range of variation. Among the major goals of this paper are the summarization of this variation for all important character fields; the polarization of character states for as many different characters as possible for which there are reliable and extensive data; and the clear indication of important gaps in the existing data base. In the second half of the paper, the results of a manual cladistic analysis, based on the foregoing conclusions, are discussed as they pertain to aroid taxa accepted a priori as natural; a preliminary intrafamilial cladogram, reflecting these considerations, is offered; and a new infrafamilial classification based on this cladogram is proposed.

History of Classification of the Araceae

The history of internal aroid classification has been reviewed by Nicolson (1960a, 1987), from which much of what follows is abstracted.

All familiar classifications of the Araceae can be conveniently reduced to two origins: the Schottian school and the Englerian school. The classification of Schott (1860) was the first in which the Araceae were treated as a single unit substantially equivalent with that recognized today. This highly subdivided system was based primarily on floral morphology and employed a comparatively narrow generic concept. Only the curious aquatic genus *Pistia*, of the genera then known, was not yet included in the family. Authors prior to Schott did not necessarily recognize an Araceae coextensive with the one accepted today, and some (e.g., Lindley, 1847) segregated the genera then known into two or three different families, attributing substantially different affinities to each.

Engler's (1876) first critical classification of the Araceae was already substantially the same as his now familiar scheme, except that in 1876 10 subfamilies were recognized instead of the present eight. *Pistia* was included as an aroid for the first time, and "Lemnoideae" was included as a subfamily of Araceae.

Hooker (1883) adapted and modified Schott's system, adopting many of Engler's generic concepts. Hooker divided the Araceae into 11 tribes; he included *Pistia* in his tribe Arinae but excluded the "Lemnoideae" from the family.

Engler's own system was refined in subsequent publications, culminating in his final major treatment of the family, partly with Krause, which appeared in *Das Pflanzenreich* from 1905 to 1920 (see Engler, 1920b, for a summary of the system). It was updated and slightly modified by Bogner in 1978 and miscellaneous subsequent papers (see especially Bogner, 1985b; Bogner et al., 1985), in which form it appears in Table 1 (with suprageneric nomenclature adjusted according to Nicolson, 1984b). Engler's classification scheme is considerably different from those of the Schottian school and places a strong emphasis on vegetative morphology and anatomy.

The little-known system of Hotta (1970) is a spinoff of Engler's system, in which three of Engler's subfamilies are submerged: Monsteroideae into Pothoideae, Colocasioideae into Philodendroideae, and Calloideae partly (Orontieae) into Lasioideae and partly (*Calla*) into Philodendroideae. One new subfamily (Acoroideae s.s.) is recognized, for a total of six subfamilies.

Hutchinson's (1973; Appendix 1) system represents the most modern incarnation of the Schottian school of aroid classification, and, as such, is based mainly on floral morphology. An extension and elaboration of Hooker's system, Hutchinson's classification utilizes 18 tribes as the major subdivisions.

Although Hutchinson's system is still occasionally employed in certain contexts (e.g., by Raven & Axelrod, 1974), virtually all major contemporary aroid workers are of the Englerian school. The most recent refinement of the Englerian system is that of Bogner & Nicolson (in press), in which the tribe Acoreae is elevated to subfamilial rank, and a few lesser taxa are transferred from one subfamily to another. Most basic Englerian concepts, however, remain intact. Engler's system (Table 1) has also been used as a convenient framework of ref-

TABLE 1. The aroid classification of Engler[1].

Taxa	Numbers of species	Ranges	Placements in this paper
Subfamily Pothoideae (properly Acoroideae)[2]			
Tribe Potheae[2]			
Pothos L.	50	Southeast Asia	Pothoideae
Pothoidium Schott	1	Southeast Asia	Pothoideae
Pedicellarum M. Hotta	1	Southeast Asia	Pothoideae
Anadendrum Schott	9	Southeast Asia	Pothoideae
Tribe Heteropsideae			
Heteropsis Kunth	12	Neotropics	Pothoideae
Tribe Anthurieae			
Anthurium Schott	700–1,000	Neotropics	Pothoideae
Tribe Culcasieae			
Culcasia P. Beauv.	20	Africa	Philodendroideae
Tribe Zamioculcadeae[2]			
Zamioculcas Schott	1	Africa	Pothoideae
Gonatopus Hook. f.	7	Africa	Pothoideae
Tribe Acoreae			
Acorus L.	2–6	North Temperate	excluded from Araceae
Gymnostachys R. Br.	1–2	Australia	Pothoideae
Subfamily Monsteroideae			
Tribe Monstereae			
Rhaphidophora Hassk.	60	Asia, Africa	Pothoideae
Epipremnum Schott	15	Southeast Asia	Pothoideae
Amydrium Schott	8	Southeast Asia	Pothoideae
Scindapsus Schott	25	Asia	Pothoideae
Alloschemone Schott	1	South America	Pothoideae
Stenospermation Schott	20	Neotropics	Pothoideae
Rhodospatha Poeppig	15	Neotropics	Pothoideae
Monstera Adans.	22†	Neotropics	Pothoideae
Tribe Spathiphylleae			
Spathiphyllum Schott	45	Neotropics, Southeast Asia	Pothoideae
Holochlamys Engl.	5	Southeast Asia	Pothoideae
Subfamily Calloideae			
Tribe Symplocarpeae (properly Orontieae)[2]			
Lysichiton Schott	2	North Temperate	Lasioideae
Symplocarpus Salisb. ex Nutt.	1–3	North Temperate	Lasioideae
Orontium L.	1	North America	Lasioideae
Tribe Calleae			
Calla L.	1	North Temperate	Philodendroideae[2]
Subfamily Lasioideae			
Tribe Lasieae			
Subtribe Lasiinae (properly Dracontiinae)[2]			
Cyrtosperma Griffith[3]	11	Southeast Asia	Lasioideae
Lasia Lour.	3	Southeast Asia	Lasioideae
Anaphyllum Schott	2	India	Lasioideae
Podolasia N. E. Br.	1	Southeast Asia	Lasioideae
Urospatha Schott	20	Neotropics	Lasioideae
Dracontioides Engl.	1	South America	Lasioideae
Echidnium Schott	(2)	South America	Synonym of *Dracontium*[3]
Dracontium L.	15	Neotropics	Lasioideae

TABLE 1. Continued.

Taxa	Numbers of species	Ranges	Placements in this paper
Subtribe Pycnospathinae			
Pycnospatha Thorel ex Gagnepain	2	Southeast Asia	Lasioideae
Tribe Pythonieae (properly Thomsonieae)[2]			
Pseudohydrosme Engl.	2	Africa	Philodendroideae
Anchomanes Schott	10	Africa	Philodendroideae
Plesmonium Schott	(2)	South Asia	Synonym of *Amorphophallus*[5]
Thomsonia Wallich	(2)	South Asia	Synonym of *Amorphophallus*[5]
Pseudodracontium N. E. Br.	7	Southeast Asia	Aroideae
Amorphophallus Blume ex Decne.	100	Asia, Africa, Australia	Aroideae
Tribe Nephthytideae			
Nephthytis Schott	7	Africa	Philodendroideae
Cercestis Schott	12	Africa	Philodendroideae
Rhektophyllum N. E. Br.	(2)	Africa	Synonym of *Cercestis*[4]
Tribe Montrichardieae			
Montrichardia Crüger	3	Neotropics	Philodendroideae
Subfamily Philodendroideae			
Tribe Philodendreae			
Subtribe Homalomeninae			
Furtadoa M. Hotta	2[6]	Southeast Asia	Philodendroideae
Homalomena Schott	140	Southeast Asia, Neotropics	Philodendroideae
Diandriella Engl.	(1)	New Guinea	Synonym of *Homalomena*[4]
Subtribe Schismatoglottidinae			
Schismatoglottis Zoll. & Moritzi	100	Southeast Asia, South America	Philodendroideae
Bucephalandra Schott	2[7]	Southeast Asia	Philodendroideae
Phymatarum M. Hotta	2	Southeast Asia	Philodendroideae
Aridarum Ridley	7	Southeast Asia	Philodendroideae
Heteroaridarum M. Hotta	1	Southeast Asia	Philodendroideae
Hottarum Bogner & Nicolson	4[7]	Southeast Asia	Philodendroideae
Piptospatha N. E. Br.	10	Southeast Asia	Philodendroideae
Subtribe Philodendrinae			
Philodendron Schott	350–600	Neotropics	Philodendroideae
Tribe Anubiadeae			
Anubias Schott	14	Africa	Philodendroideae
Tribe Aglaonemateae			
Aglaonema Schott	21	Southeast Asia	Philodendroideae
Aglaodorum Schott	1	Southeast Asia	Philodendroideae
Tribe Bognereae[2]			
Bognera Mayo & Nicolson	1	South America	Philodendroideae
Tribe Dieffenbachieae			
Dieffenbachia Schott	30+	Neotropics	Philodendroideae
Tribe Zantedeschieae			
Zantedeschia Sprengel	6	Africa	Philodendroideae

TABLE 1. Continued.

Taxa	Numbers of species	Ranges	Placements in this paper
Tribe Typhonodoreae			
Typhonodorum Schott	1	Africa	Philodendroideae
Tribe Peltandreae			
Peltandra Raf.	2	North America	Philodendroideae
Subfamily Colocasioideae			
Tribe Colocasieae (properly Caladieae)[2]			
Subtribe Steudnerinae			
Steudnera K. Koch	8	Southeast Asia	Colocasioideae
Remusatia Schott	2	South Asia, Africa	Colocasioideae
Gonatanthus Klotzsch	3	South Asia	Colocasioideae
Subtribe Hapalininae			
Hapaline Schott	5	Southeast Asia	Colocasioideae
Subtribe Caladiinae			
Jasarum Bunting	1	South America	Colocasioideae
Scaphispatha Brongn. ex Schott	1	South America	Colocasioideae
Caladium Vent.	8	Neotropics	Colocasioideae
Aphyllarum S. Moore	1	South America	Colocasioideae
Chlorospatha Engl.	16	Neotropics	Colocasioideae
Xanthosoma Schott	45	Neotropics	Colocasioideae
Subtribe Colocasiinae			
Colocasia Schott	8	Southeast Asia	Colocasioideae
Subtribe Alocasiinae			
Alocasia (Schott) Don	70	Southeast Asia	Colocasioideae
Xenophya Schott	(2)	Southeast Asia	Synonym of *Alocasia*[8]
Tribe Syngonieae			
Syngonium Schott	33	Neotropics	Colocasioideae
Tribe Ariopsideae			
Ariopsis Nimmo	1	Southeast Asia	Aroideae
Subfamily Aroideae			
Tribe Stylochaetoneae			
Stylochaeton Lepr.	21	Africa	Lasioideae
Tribe Arophyteae			
Carlephyton Jum.	3	Madagascar	Philodendroideae
Colletogyne Buchet	1	Madagascar	Philodendroideae
Arophyton Jum.	7	Madagascar	Philodendroideae
Tribe Asterostigmateae (properly Spathicarpeae)[2]			
Mangonia Schott	2	South America	Philodendroideae
Taccarum Brongn. ex Schott	5	South America	Philodendroideae
Asterostigma Fischer & C. Meyer	7	South America	Philodendroideae
Gorgonidium Schott	3	South America	Philodendroideae
Synandrospadix Engl.	1	South America	Philodendroideae
Gearum N. E. Br.	1	South America	Philodendroideae
Spathantheum Schott	2	South America	Philodendroideae
Spathicarpa Hook.	7	South America	Philodendroideae

TABLE 1. Continued.

Taxa	Numbers of species	Ranges	Placements in this paper
Tribe Protareae			
Protarum Engl.	1	Seychelles	Colocasioideae
Tribe Callopsideae			
Callopsis Engl.	1	Africa	Philodendroideae
Tribe Zomicarpeae			
Zomicarpa Schott	3	South America	Colocasioideae
Zomicarpella N. E. Br.	2	South America	Philodendroideae[9]
Filarum Nicolson	1	South America	Philodendroideae
Ulearum Engl.	2	South America	Philodendroideae
Tribe Areae			
Subtribe Arinae			
Arum L.	24	Eurasia	Aroideae
Dracunculus Miller	2	Mediterranean	Aroideae
Helicodiceros Schott	1	Mediterranean	Aroideae
Theriophonum Blume	5	India	Aroideae
Typhonium Schott	25	Southeast Asia, East Asia, Australia	Aroideae
Sauromatum Schott	6	South Asia, Africa	Aroideae
Eminium (Blume) Schott	7	West Asia, Central Asia	Aroideae
Biarum Schott	16	Mediterranean	Aroideae
Subtribe Arisarinae			
Arisarum Miller	3	Mediterranean	Aroideae
Subtribe Arisaematinae			
Arisaema C. Martius	150	Africa, Asia, North America	Aroideae
Subtribe Pinelliinae (properly Atherurinae)[2]			
Pinellia Ten.	7	East Asia	Aroideae
Subtribe Ambrosininae			
Ambrosina Bassi	1	Mediterranean	Aroideae
Subtribe Cryptocoryninae			
Lagenandra Dalz.	12	South Asia	Aroideae
Cryptocoryne Fischer ex Wydler	50	Southeast Asia	Aroideae
Subfamily Pistioideae			
Pistia L.	1	Pantropical	Aroideae

[1] (1920b; as modified by Bogner (1978) and miscellaneous subsequent papers). Species numbers and geographic range data are mainly from Croat (1979). Only the most general indication of the geographic range is given for each genus.

[2] See Nicolson (1984b); Philodendroideae sensu this paper (including *Calla*) is properly Calloideae.

[3] African and South American species formerly included in *Cyrtosperma* are now assigned to *Lasiomorpha* Schott (1 sp.) and *Anaphyllopsis* A. Hay (3 spp.), respectively (Hay, 1988).

[4] See Bogner (1985b).

[5] See Bogner et al. (1985).

[6] See Hotta (1985).

[7] See Bogner (1984).

[8] See Hay (in press).

[9] J. C. French (pers. comm.) reported secretion tubes from a second species of *Zomicarpella* recently discovered in Brazil by J. Bogner. Pollen of this species, as judged from unpublished SEM micrographs, more closely resembles pollen of *Zomicarpa* than that of *Filarum* or *Ulearum*. Thus, *Zomicarpella* may belong in Colocasioideae.

erence in the present paper; however, this should not be taken to imply prejudice in favor of that scheme. The vindication of one or another established system of classification has not been an objective of the present study. Rather, the phylogeny of Araceae is emphasized, with a view to deduce a defensible cladogram which can ultimately become the foundation for a new classification. But it is clear from the outset that many more of Engler's than of Hutchinson's tribes are natural groups, although, as will be seen, Engler's subfamilies are not so robust.

The suprageneric aroid taxa referred to in the text that follows are those of Engler (1920b), as modified by Bogner (1978), and include nomenclatural changes mandated by Nicolson (1984b). In Tables 2 and 3 aroid genera have been assigned to subfamilies according to the new system (the linear order within these subfamilies being of no great significance, although accepted tribes are maintained intact). Table 1 provides a cross-reference between the new system and the more familiar neo-Englerian scheme.

Fossil History of the Araceae

The fossil record of monocots has been reviewed by Daghlian (1981), and the macrofossil record of Araceae partially reviewed by Gregor & Bogner (1984). Macrofossils clearly show that the Araceae were already fairly diverse and well advanced by the early Tertiary. At least four modern subfamilies were represented by the Oligocene. At least two modern genera (*Philodendron* and *Peltandra*) are known from the Eocene, and Gregor & Bogner (1984) listed six others (*Pistia*, *Arisaema*, *Lysichiton*, *Stenospermation*, *Orontium*, and *Calla*) known from unspecified Tertiary epochs. There is one tentatively acceptable aroid fossil from the Paleocene of Central Asia, which would be the earliest record attributable to the family. Crepet (1978) suggested that the Araceae radiated in the late Cretaceous or Paleocene.

Dilcher & Daghlian (1977) presented evidence of the presence of *Philodendron* subg. *Meconostigma* in the Eocene of Tennessee, based on fossilized leaves; Mayo (1986), however, suggested these might belong to Peltandreae. Bogner (1976b) attributed a spadix preserved in Eocene amber to the tribe Monstereae. Madison & Tiffney (1976) surveyed the fossil record of seeds attributed to the Monstereae, and concluded that some fossils could be accommodated in that tribe but assigned others to the Pothoideae or Lasioideae; a few were interpreted as not being aroids. These records were mainly from the Oligocene or earlier.

The pollen fossil record, according to the review of Muller (1981), does not reveal much about the family Araceae. Pollen (*Liliacidites*) representing a type known only in monocots extends back to the very early Cretaceous (Aptian) (Doyle, 1973; Wolfe et al., 1975; Walker & Walker, 1984), yet pollen assignable to extant monocot families does not appear until the late Cretaceous (Maestrichtian) (Muller, 1981). Most Cretaceous monocot pollen is of a general type (reticulate, monosulcate) known from many extant monocot families, and until an extensive survey of modern monocot pollen is available, little use can be made of it at the family level (Daghlian, 1981).

The only aroid pollen that can be recognized in the fossil record is the distinctive striate *Spathiphyllum* type (Muller, 1981). This type of pollen is known from Mexico, Colombia, and Palau (all within the contemporary range of the genus), only as far back as the Miocene. It is perhaps significant that the easily identifiable pollen of *Spathiphyllum* has not turned up in earlier deposits, and that other distinctive types of aroid pollen, such as the reticulate, forate *Anthurium* type, have not yet been reported in the fossil record.

Character Variation and Polarization

geographical distribution

The distribution of Araceae was briefly outlined in the introduction and has been covered in detail by Croat (1979), Grayum (1984), and Bogner (1987). Table 1 provides a brief description of the range of each aroid genus.

The Araceae are overwhelmingly tropical, with only a few truly temperate genera—all of these in the Northern Hemisphere. The poleward attenuation of the aroid flora is well exemplified by floristic data from South America: whereas the flora of Venezuela contains nearly 200 species of Araceae (Bunting, 1979), there are only 17 in the flora of Argentina (Crisci, 1971), and only the cosmopolitan *Pistia stratiotes* occurs in Chile (Marticorena & Quezada, 1985).

The Asian tropics have the largest number of genera (44); the Neotropics have about 36 genera, but a higher percentage of these are endemic, and the Neotropics have significantly more species (Croat, 1979). The African aroid flora, with just 20 genera, is relatively impoverished, as is frequently the case with other tropical wet-forest taxa.

Aroid genera tend to be restricted to major phytogeographical realms. With Hay's (1988) recent fragmentation of *Cyrtosperma*, the monotypic, cosmopolitan and artificially spread *Pistia* remains

as the only pantropical aroid genus. *Arisaema* occurs principally in temperate to subtropical regions but has extended sparingly into central Africa, Southeast Asia, and Mexico. *Calla*, *Symplocarpus*, and *Lysichiton* occur in temperate or boreal regions of North America and Eurasia.

Few genera are shared between any two tropical realms. *Spathiphyllum*, *Homalomena*, *Schismatoglottis*, and perhaps *Scindapsus* are common to Southeast Asia and the Neotropics, and are absent from Africa. *Rhaphidophora*, *Sauromatum*, *Pothos*, *Amorphophallus*, and *Remusatia* occur in Africa and Eurasia (and the latter three in Australia as well); however, in the cases of *Remusatia* and *Sauromatum* (and of *Pothos* in Africa) we are clearly dealing with recent dispersal of a single, presumably highly vagile species. *Epipremnum* and *Typhonium* occur naturally in Eurasia and Australia. No genera are shared solely by Africa and Australia, nor by Africa and the Neotropics.

Only two natural tribes, Monstereae and Lasieae, are pantropical (though represented in Africa by just two and one species, respectively). In both cases, the African species are more closely related to Asian than American elements (Grayum, 1984). The Englerian subtribe Arinae, a closely knit group of eight genera, has a strikingly Tethyan distribution: from western Europe and the Canary Islands, throughout the Mediterranean region, and eastward to Hupeh, the Philippines, New Guinea, and Queensland.

Several smaller geographical regions harbor concentrations of endemic aroid taxa. For example, *Anaphyllum*, *Theriophonum*, *Lagenandra*, and two sections of *Amorphophallus* are endemic to southern India and Sri Lanka. *Pedicellarum* and five genera of subtribe Schismatoglottidinae are endemic to Borneo, and a single genus each to Sumatra (*Furtadoa*) and New Guinea (*Holochlamys*). *Pinellia* and *Amorphophallus* sect. *Dysamorphophallus* are strictly East Asian. *Pseudohydrosme*, *Anchomanes*, *Nephthytis*, *Cercestis*, *Anubias*, and two sections of *Amorphophallus* are restricted to tropical West Africa. *Typhonodorum* and all three genera of the tribe Arophyteae are Madagascan (the former also occurring, perhaps adventively, in East Africa and Mauritius). *Protarum* is unique in being endemic to the Seychelles, *Gymnostachys* to Australia.

In the New World, *Orontium* and *Peltandra* are confined to eastern North America. The tribes Spathicarpeae and Zomicarpeae occur in a zone fringing the Amazon basin, from Bahia on the east coast of Brazil, southward across northern Paraguay and Bolivia, and northward along the Andean foothills. The New World members of tribe Lasieae show vestiges of a similar distribution. *Jasarum* is the only aroid genus restricted to the Guayana Shield.

Additional biogeographical details relevant to particular genera can be found in the second half of this paper.

The geographic distribution of the Araceae is complicated and difficult to interpret. Willis (1949), on the basis of his pre-plate tectonics biogeographical analysis of the family, suggested that the Araceae are polyphyletic. Raven & Axelrod (1974), with the benefit of plate tectonic theory (though perhaps handicapped by their use of Hutchinson's tribal classification), aptly described the distribution of Araceae as "West Gondwanalandic-Laurasian." No Araceae can definitely be traced to an East Gondwanalandic origin (*Gymnostachys* and *Protarum* being perhaps the best candidates). The pantropical distribution of certain indisputably natural aroid taxa—e.g., the tribes Lasieae and Monstereae—strongly suggests that the family was well established in tropical West Gondwanaland prior to the separation of Africa from South America. The alternative hypothesis, that South America and Africa were colonized separately from Laurasia following the breakup of West Gondwanaland, seems highly unlikely in light of the long-standing separation of North and South America (from the Jurassic to about the Oligocene; see Raven, 1979). The "relict" distribution patterns of such phenetically primitive groups as Spathicarpeae and Lasieae in South America, and Zamioculcadeae in Africa, imply a Gondwanalandic origin for these taxa as well.

It seems probable, then, that Araceae were present in West Gondwanaland at an early date and radiated there, with some of these elements ultimately reaching tropical Asia by way of Africa. That African members of Monstereae and Lasieae appear more closely related to their Asian than neotropical counterparts may be evidence of this. These migrations may have taken place during the late Cretaceous or, more likely, in the Paleocene or Eocene, at which times the two land masses appear to have been connected (Raven, 1979). The African aroid flora was presumably severely depleted due to the aridity of Neogene and Quaternary times (Raven & Axelrod, 1974), with some groups (Spathiphylleae, *Philodendron*, Peltandreae, Colocasioideae) pushed out or extirpated and the remainder restricted to refugia or subjected to heavy selective pressures.

But the early presence of Araceae in West Gondwanaland does not establish a Gondwanalandic

origin for the family. Though extant north-temperate Araceae are few, phenetically (and presumably cladistically) primitive taxa are disproportionately represented among them: notably the four genera of Engler's subfamily Calloideae, plus Acoraceae, a putative sister taxon to Araceae. Also noteworthy in this connection is the absence of Araceae in the truly temperate Southern Hemisphere; i.e., if Araceae originated in tropical West Gondwanaland and later extended into the north-temperate realms, why did the family not simultaneously extend southward? Thus it is perhaps reasonable to propose that the Araceae originated in temperate or subtropical Laurasia, then reached West Gondwanaland via Eurasia (the North American route having been unavailable) at an early date (late Cretaceous?) and underwent a major radiation in West Gondwanaland. Some elements of this Gondwanalandic aroid flora then migrated secondarily into Eurasia, a few (*Philodendron*, *Peltandra*, *Orontium*?) even reaching North America via the North Atlantic route—this having been the main route prior to the Eocene (Raven & Axelrod, 1974; Wolfe, 1975), which is the age of the Tennessee *Philodendron* fossil discussed earlier. The present confinement of *Peltandra* and *Orontium* to the eastern United States perhaps reflects the barrier imposed by a north–south epicontinental seaway in the Great Plains region up to the Paleocene (Wolfe, 1975), and subsequent climatic changes.

The Tethyan distribution of Engler's subtribe Arinae may reflect a proximal Laurasian origin for this group. Presumably, the ancestral Araceae did not migrate en masse from Laurasia into West Gondwanaland; some remained behind. These primal Laurasian elements, later isolated from their Gondwanalandic counterparts by the Tethys Sea, may then have undergone a radiation of their own in the warm, subtropical forests that prevailed, by the Eocene, along the northern margin of that sea from Western Europe to Indomalaysia (Wolfe, 1975). In addition to the Arinae, groups such as *Pinellia*, *Arisaema*, *Ariopsis*, *Arisarum*, *Ambrosina*, *Pistia*, and the tribe Thomsonieae are implicated in this scenario. Evidence for this interpretation includes the present diversity of these groups (especially *Arisaema* and *Amorphophallus*) in Laurasian areas, as well as their poor representation in Southeast Asia and Africa and complete absence from the Neotropics. Though the proposed Tethys radiation could have involved taxa newly emigrated from Africa, the putatively close interrelationship of the Tethyan taxa and the absence of such groups as Monsteroideae and Philodendroideae undermine that scenario.

Arisaema clearly reached North America from Eurasia (rather than vice versa), and rather recently at that; the Bering Straits route was at relatively low latitudes and became important during the Eocene and Oligocene, after the closure of the North Atlantic route (Raven & Axelrod, 1974; Wolfe, 1975). *Calla*, *Symplocarpus*, and *Lysichiton* may be subject to the same consideration.

VEGETATIVE MORPHOLOGY AND ANATOMY

Extensive summaries of aroid vegetative morphology may be found in Engler (1877, 1920b) and Grayum (1984), and of vegetative anatomy in Solereder & Meyer (1928), Grayum (1984), and, most recently, French (in press). Only the most basic and phylogenetically significant features will be discussed here. Table 2 provides overviews of important anatomical features.

Germination. Germination in most aroids is cryptocotylar, or hypogeal (Boyd, 1932; Dahlgren & Clifford, 1982), although in *Arum* and *Philodendron* it is perhaps epigeal. Seedling morphology in Araceae is highly variable, and has recently been surveyed by Tillich (1985; see discussion in Grayum, in press b). The cotyledon is generally similar to a foliage leaf, and in a few genera (*Eminium*, *Sauromatum*) may even be stalked—an extremely rare circumstance among monocots (Tillich, 1985). The first leaf of the plumule is usually a cataphyll (a leaf-sheath lacking a petiole and blade) but may be a foliage leaf in several genera (Engler, 1920b). The hypocotyl becomes converted into a corm or tuber in *Pinellia*, however the latter organ is of epicotylar origin in *Arum*, *Arisaema*, *Arisarum*, and *Dracunculus* (Tillich, 1985). As is typical of monocots, the radicle is short-lived, subsequent roots arising adventitiously from the stem (French, in press).

Shoot development and morphology. Aroid shoot development has been freshly interpreted and summarized by Ray (1987b). Growth of the main axis in Araceae, at least up to the time of the initial flowering episode, is always monopodial. After flowering, growth is sympodial, with four exceptions: in *Pothos*, *Pothoidium*, *Heteropsis*, and presumably *Pedicellarum*, monopodial growth continues exclusively. The inflorescences in these genera are terminal (as in all Araceae) on determinate side shoots, and not axillary as incorrectly described in some previous interpretations.

Ray (1987b) recognized three major categories of sympodial growth in Araceae: anisophyllous, in which the articles (a stem section produced from a single meristem, from its inception to its termination in a developed or aborted inflorescence) have a variable number of leaves, whether foliage leaves or cataphylls; homeophyllous, in which the articles have a fixed number of leaves; and intermittent homeophyllous, in which the above two types of sympodial growth alternate. Since the homeophyllous phase in intermittent homeophyllous growth is mainly associated with active flowering, this category will be discussed in a later section.

Anisophyllous sympodial growth occurs in a wide range of aroid subtaxa (listed in Ray, 1987b) and is probably the most primitive growth type within the family. Its distribution shows some taxonomically intriguing patterns; anisophyllous growth is, for example, restricted in *Anthurium* to sect. *Polyphyllium*, and in *Philodendron* to subg. *Pteromischum*. Some species of the latter taxon exhibit proleptic renewal—i.e., the renewal shoots develop from a bud that has rested, relative to the parent shoot (Ray, 1987a). (Earlier incorrect interpretations of this phenomenon [Madison, 1978a; Blanc, 1980] characterized growth in subg. *Pteromischum* as monopodial [Ray, 1987b].) Sympodial growth in all other Araceae is sylleptic (the bud does not rest relative to the parent shoot), with the apparent exception of a few species of *Monstera* (Ray, 1988).

Various subtypes of homeophyllous sympodial growth may be recognized in Araceae, depending upon the number of leaves (whether foliage leaves or cataphylls) borne by each article (Ray, 1987b). Monophyllous growth is exclusively associated with the development of "second-order" inflorescences and is discussed later. Diphyllous sympodial growth is characteristic of *Philodendron* (except subg. *Pteromischum*) and also occurs in a slightly different form in *Symplocarpus*. Triphyllous sympodial growth is the rule in *Anthurium* (except sect. *Polyphyllium*) and is also known from a few other unrelated genera (Ray, 1987b). Tetraphyllous growth is exclusive to *Orontium*, and pentaphyllous growth to *Stenospermation*, where it is only imperfectly developed.

In the vast majority of aroids, each renewal shoot during sympodial growth arises in the axil of the penultimate leaf (whether foliage leaf or cataphyll) below the spathe, except in monophyllous homeophyllous growth. In *Symplocarpus* and perhaps *Lysichiton*, however, the renewal shoot regularly arises in the axil of the ultimate leaf, and in *Gymnostachys* it arises in the axil of the antepenultimate leaf before the "spathe" (interpreted here as a "mesobracteole"; Ray, 1988).

Sympodial growth predominates among monocots according to Holttum (1955), who believed it to be more primitive than monopodial growth. Moore & Uhl (1982) also believed sympodial growth to be primitive within the palms, and this is certainly the case for Araceae as well. Permanent monopodial growth may well represent a neotenic retention of this normally juvenile condition (Grayum, 1984), as also suggested by Hay (1986) and Barabé (1987).

The Araceae exhibit a great diversity of growth habits (see Grayum, 1984; Bogner, 1987), including caulescent (e.g., *Dieffenbachia*) and acaulescent (*Spathiphyllum*) herbs, pachycaulous, arborescent plants to 5 m or more in height (*Montrichardia*, *Xanthosoma*), monopodial, shrubby vines (*Pothos*), and root-climbing, sympodial vines (*Monstera*, *Philodendron*, *Syngonium*). True epiphytes (i.e., with seeds germinating on the host plant) are rare in Araceae. Only *Anthurium* and *Stenospermation* consist largely of epiphytic species. *Pistia stratiotes* is unique in being a floating aquatic.

The two most common growth habits in Araceae, at the generic level, are the rhizomatous and tuberous (or cormose) forms. These types are in general easily distinguished, although short and thick and even erect (as in *Symplocarpus* and *Podolasia*) so-called rhizomes may blur the distinction. In general, rhizomatous growth habits tend to be associated with wet habitats (*Cryptocoryne*, *Jasarum*), tuberous growth with seasonally dry or arid habitats (*Biarum*, *Eminium*). Yet both types sometimes occur in the same genus (*Stylochaeton*, *Arophyton*, *Arisaema*) or even species, as in *Arisarum vulgare* (Galil, 1978) and *A. simorrhinum* (Herrera, 1988).

The development of "tubers" and "rhizomes" in Araceae is little understood, as is the case for monocots in general (Tomlinson, 1970). Aroid organs customarily classed in one or another of these two categories are not necessarily homologous. Hotta (1971) and Tillich (1985) distinguished two types of tuber development in the Araceae but did not review their distribution comprehensively.

What might the growth habit of the hypothetical aroid ancestor have been? The question is difficult but one can begin by eliminating the more obviously specialized forms: tuberous geophytes, epiphytes, floating aquatics, monopodial vines, and probably even sympodial vines (Hotta, 1971; Ray, 1989).

Workers on Liliales (Schlittler, 1955; Conover, 1983) have concluded that nonrhizomatous forms with much-branched, leafy stems (resembling the modern-day Philesiaceae) represent the primitive type from which arborescent and ultimately rosette forms were derived via condensation of the axis and other changes. Tomlinson (1962), by contrast, believed that arborescent forms are primitive in Zingiberales, and that herbaceous and vining forms arose partly via neoteny. This agrees with Corner's (1954) controversial "Durian Theory," which dictates that a "stout pachycaul stem with large compound leaves was the ancestral growth form of the Arales." See Hay (1986) for a full-blown application of the Durian Theory to aroid phylogenetics.

I believe that the rhizomatous, or perhaps erect caulescent, growth habit is basic to Araceae. These appear to be the most "flexible" growth forms in the family, i.e., those from which all of the more extreme forms might have been derived in the most parsimonious manner. The rhizomatous habit is particularly widespread and occurs in many ostensibly primitive groups—e.g., *Gymnostachys*, the Orontieae, Lasieae, and others. The derivation of tuberous from rhizomatous forms seems but a short step, and Li (1980) proposed such an interpretation for *Arisaema*.

Leaf morphology. Aroid leaves are always alternate and when fully developed typically consist of a sheath, petiole, and lamina. Ray (1987a) recently reviewed aroid leaf types and presented a detailed classification based on morphology and function. His three main morphological types are: foliage leaves, which are unreduced (generally with all three of the above parts represented); reduced leaves, 10–70% the size of foliage leaves on the same plant and usually with the lamina very small to obsolete; and cataphylls, reduced to less than 10% and generally consisting of just a sheath.

The first leaf on a new vegetative axis is called the prophyll, which is a cataphyll in all Araceae except *Gymnostachys*, *Orontium*, and *Symplocarpus*, in which it is a foliage leaf (Ray, 1988). The leaf subtending an inflorescence within a compound inflorescence is termed a bracteole; bracteoles are apparently always cataphylls. Prophylls and bracteoles are morphologically indistinguishable (Ray, 1987a); both have a two-keeled structure, as is typically the case for monocots in general, whereas cataphylls in other positions generally have a single keel.

The leaf immediately following the prophyll is termed a mesophyll; by analogy, the leaf immediately following the bracteole is called a mesobracteole (the latter are known definitely only in *Gymnostachys*, where they are cataphylls). The mesophyll is frequently a cataphyll or reduced leaf. In such cases, additional cataphylls or reduced leaves may follow; these are also referred to as mesophylls.

Prophylls, bracteoles, mesophylls, and mesobracteoles may be described as either "sylleptic" or "proleptic" inasmuch as the characteristics of these leaf types may differ depending on the type of growth involved. For example, proleptic prophylls are usually tiny, and the proleptic mesophylls numerous; sylleptic prophylls, on the other hand, are comparatively large, and the sylleptic mesophyll is generally solitary and often a foliage leaf (Ray, 1987a).

The leaf subtending the inflorescence, whether developed or aborted, in sympodial growth is termed a sympodial leaf. Although sympodial cataphylls occur, this is usually a foliage leaf in which the sheath is rudimentary and the petiole base does not encircle the stem. In species of *Philodendron* with diphyllous sympodial growth (i.e., the entire genus apart from subg. *Pteromischum*), all of the foliage leaves beyond the juvenile monopodial phase are sympodial leaves, most of which subtend aborted inflorescences. The same is true of those sections of *Anthurium* with triphyllous growth (i.e., all except sect. *Polyphyllium*), since both the prophyll and mesophyll are always cataphylls (Ray, 1988).

Any leaves between the mesophyll(s) and the sympodial leaf are termed monopodial leaves. These are almost always foliage leaves, usually with a well-developed sheath and a base encircling the stem. The morphological differences between sympodial and monopodial leaves facilitate the differentiation of juvenile from adult plants in many aroid genera, even in the absence of developed inflorescences.

Other, more specialized leaf types, including reduced leaves or cataphylls associated with dispersal shoots ("flagelles") and dormancy, were discussed by Ray (1987a).

Intravaginal squamules, characteristic of the Zosterales, are known in just a few genera of Araceae: some *Philodendron* species (Engler, 1912; Ritterbusch, 1971; Blanc, 1977) and apparently also *Cryptocoryne* and *Lagenandra* (Engler, 1920a).

Phyllotaxy in Araceae may be either distichous or spiral (helical). Spirally arranged leaves almost always diverge at 2/5. Distichous leaves occur almost exclusively in the subfamilies Pothoideae, Monsteroideae, and Calloideae (Grayum, 1984). Outside these subfamilies, only *Heteroaridarum* (Hotta, 1976) and a single species of *Aridarum*

(Bogner, 1981b), both in Philodendroideae, are known to possess distichous leaves.

Distichy, in monocots, is characteristic of such groups as Gramineae, Orchidaceae, Zosterales, and Zingiberales. It is unknown in Pandanaceae, rare in Palmae, and known from just four genera in Cyclanthaceae. Some authors (e.g., Harling, 1958) have assumed that distichy is primitive in seed plants. Beck et al. (1982), however, concluded that spiral phyllotaxy is more primitive—another cornerstone of the "Durian Theory" (Corner, 1954). Dahlgren & Clifford (1982) suspected that spiral phyllotaxy is basically primitive but that it may have been secondarily derived in some cases. The distribution of distichy in Araceae suggests that the latter may be the case here. That the first leaves of araceous shoots are nearly always distichous, even in species with ultimately spiral phyllotaxy (Engler, 1877), may be germane in this connection. Furthermore, Periasamy & Muruganathan (1986) reported that the phyllotaxy of leaf primordia in *Arisaema* is distichous. Tomlinson (1966) has suggested that distichy in Commelinaceae may have come about via neoteny, a hypothesis that ought to be considered for Araceae as well. Most Araceae with distichous leaves are climbers, so there is probably also a functional correlation.

Modifications of the leaf sheath are rare in Araceae. In a few taxa, such as *Calla*, some *Philodendron* species, and several Schismatoglottidinae, the sheath is free at the tips and has been referred to as a "ligule-" or "stipulelike" structure (Dahlgren & Clifford, 1982; French, in press).

The most important petiole character in Araceae is the presence or absence of a geniculum. A geniculum (pulvinus) at the apex of the petiole occurs in most Pothoideae and throughout Monsteroideae (see Grayum, 1984), i.e., mostly in vining genera. In Zamioculcadeae and some species of *Anthurium* (e.g., *A. oerstedianum*) the geniculum is located in the middle of the petiole. Outside of these subfamilies, genicula are extremely rare (*Anubias*, some species of *Homalomena*, perhaps some species of *Philodendron*).

All aroid leaf blades are homologous structures, and, though they may superficially resemble dicot leaves, develop in a manner typical of monocots (Kaplan, 1973).

Aroid leaves typically undergo heteroblastic development, that is, there is a marked but gradual change in morphology from juvenile to adult forms. Only a few vining genera (*Pothos*, *Rhaphidophora*, *Monstera*) show true heterophylly, defined as an abrupt switch from juvenile leaves to very different adult leaves.

Ptyxis in Araceae is supposed to be exclusively supervolute according to Cullen's (1978) survey of 16 genera representing every subfamily except Pistioideae. But involute ptyxis is now known to characterize *Lagenandra* (de Wit, 1978) and *Anthurium* sect. *Pachyneurium* (Croat & Sheffer, 1983). Supervolute ptyxis is the most frequent condition among monocots and is to be regarded as primitive for Araceae.

Although lobed and compound laminae are common in Araceae, leaf margins are otherwise virtually always entire; serrate margins are extremely rare, known only in a few species of *Arisaema*, and are certainly derived (see Hickey, 1978).

Peltate leaves occur chiefly in Engler's subfamily Colocasioideae (Grayum, 1984). This condition is exceedingly rare in other subfamilies, known from a single species each of *Anthurium*, *Philodendron*, and *Pinellia* (P'ei, 1935), and from two species of *Homalomena* sect. *curmeria* (but see also *Ariopsis*).

Lamina shape is highly variable in Araceae and has been discussed in depth by Grayum (1984) and Bogner (1987). Linear, lanceolate, elliptic, ovate, cordate, sagittate, hastate, pedately compound, and palmately (or radiately) compound leaves are widespread, and most or all of these shapes may occur even within single genera (*Philodendron* and especially *Anthurium*). Other types are less common. The narrowly linear, grasslike leaves of *Gymnostachys* are unique within the family. Truly pinnate leaves, in the dicot sense, i.e., with the leaflets abscising individually, are known only from *Zamioculcas* (once-pinnate) and *Gonatopus* (bi- or tripinnate). These genera prove inaccurate the assertion of Dahlgren & Clifford (1982) that such leaves do not exist among monocots. Pinnately or even bipinnately lobed leaves are more common, occurring commonly in Monsteroideae and sparingly in most other subfamilies.

The development of leaf pinnation in various aroid subgroups is not homologous. In Monsteroideae, pinnate leaves result from a necrotic process in which growth stops and tissue rots away (Schwarz, 1878; Ertl, 1932; Hotta, 1971; Madison, 1977). Apparently, the unusual decompound leaves of *Anchomanes* and presumably *Pseudohydrosme* also develop in this fashion (Riedl, 1978), as do leaf fenestrations in many Monsteroideae (Madison, 1977).

Pinnation in *Philodendron* is achieved by means of differential growth rates. This "marginal type" process is also involved in the development of some palmately lobed aroid leaves, as well as in more complex situations, and is characteristic of several

Lasioideae, Colocasioideae, and Aroideae, including the tribe Spathicarpeae (Ertl, 1932; Hotta, 1971; Riedl, 1978; Periasamy & Muruganathan, 1986).

The complex, deeply lobed leaves of many Lasieae in which the lamina is basically trisect with the main divisions further divided (pedately and/or pinnately) may represent a distinctive type. Here the early stages of adult leaves possess three distinct leaflet primordia, which are subsequently further dissected, presumably via the marginal process, at least in Thomsonieae.

Pedately compound or pedately lobed leaves are particularly common in Colocasioideae and Aroideae. Their development, at least in some cases, is known to involve marginal dissection (Ertl, 1932; Periasamy & Muruganathan, 1986). Curiously, pedate and tripartite leaves in Colocasioideae are restricted to New World genera (*Chlorospatha*, *Caladium*, *Xanthosoma*, *Syngonium*; but see also *Protarum*). They are more widespread in Aroideae (see Grayum, 1984). Truly palmately compound (or radiate) leaves are known with certainty only in *Anthurium* and *Arisaema*. Both of these genera also exhibit clearly pedate or pedatisect leaves, as well as tripartite leaves, which are not identifiable as pedate or palmate.

It is highly doubtful that all of these occurrences of pedate and palmate leaves can be homologized. Madison (1978b) described two distinctive heteroblastic sequences for palmate *Anthurium* species and suggested that palmate leaves may have evolved as many as seven times in this genus alone.

Hotta (1971) has contended that in aroids, "the compound leaf is apparently an evolved type originated by the dissection of a simple leaf"; this mirrors Engler's (1884) opinion on the subject. Although alternative interpretations are possible (see especially Corner, 1954; Hay, 1986; Barabé, 1987), I agree that elliptic, ovate or cordate simple leaves are the most primitive type in Araceae, and that other types, especially compound leaves, are derived. This view receives some support from the angiosperm fossil record (see Hickey, 1978). Moreover, sagittate and especially lobed and compound leaf types often seem strongly correlated, in Araceae, with condensation of the axis and often with a tuberous, geophytic habit (see Grayum, 1984). In *Biarum* and *Eminium* simple leaves probably have been derived secondarily from compound leaves.

Root morphology. For details of aroid root morphology, see the recent reviews of Grayum (1984) and French (in press). Hotta (1971) stated that "in general, the features of the root are useless for classification of the Araceae." Although this will no doubt prove to be an exaggeration, external root morphology has yielded no taxonomically useful characters to date.

Roots in all Araceae, as is typical of monocots in general, are adventitious beyond the seedling stage (Engler, 1905). Roots never become tuberous in Araceae (Hotta, 1971). In aroids with tuberous or cormose stems (many Aroideae, Lasioideae, and Calloideae), contractile roots occur and serve to pull the stem deeper into the soil (Hotta, 1971; French, in press).

Climbing and epiphytic aroids of all subfamilies typically bear aerial roots. These are frequently of two types: stout anchoring roots and longer feeder roots, which may extend to the ground from great heights. These two types differ markedly anatomically and physiologically (Lierau, 1888; see French, in press, for an exhaustive discussion). Feeder roots arise only at the nodes, whereas anchor roots may arise along the internodes as well (French, in press).

Epidermal anatomy. The epidermis of aboveground organs in Araceae is typically glabrous. Trichomes and other types of ornamentation are quite rare; their distribution, which is spotty and not of much phylogenetic significance, has been summarized by Grayum (1984) and French (in press).

The araceous cuticle shows great variation in thickness and ornamentation (Solereder & Meyer, 1928; Crepet, 1978; Behnke & Barthlott, 1983; Grau, 1983; French, in press). As yet, however, this feature has not been adequately surveyed.

Ground epidermal cells of aroid leaves are described by Grau (1983) and French (in press). Of much greater potential phylogenetic significance are stomata. One of the few generalizations that can be made concerning aroid stomata is that they exhibit the "perigeneous" type of development characteristic of monocots (Pant & Kidwai, 1966; Tomlinson, 1974), in which a sister cell of the guard cell initial becomes a neighboring cell. In all other respects, aroid stomata are quite variable. Most genera have strictly or essentially hypostomatic leaves, or else amphistomatic leaves with more stomata on the lower leaf surface (Solereder & Meyer, 1928; Pant & Kidwai, 1966; see Table 2). In *Pistia*, most stomata occur on the upper leaf surface; Pant & Kidwai (1966) interpreted this as homologous with the epistomatic condition of Lemnaceae but it is more likely an example of convergent evolution (see Grayum, 1984). Only *Orontium* has truly or essentially epistomatic leaves (Solereder & Meyer, 1928; Grear, 1973).

Among the traditional stomatal types, paracytic,

tetracytic (the hexacytic variant), and anomocytic all occur in Araceae (Stebbins & Khush, 1961; Pant & Kidwai, 1966; see Table 2), paracytic being the most frequent (contrary to Dahlgren & Clifford, 1982). Anomocytic stomata are known only in *Pistia*, all genera of the tribe Orontieae (Grear, 1973), and perhaps in some species of *Arisaema* (according to Dahlgren & Clifford, 1982). According to Stebbins & Khush (1961), paracytic stomata are primitive and the other types derived. Tomlinson (1970, 1974), however, studied the development of the stomatal apparatus in monocots and showed that the traditional system of classification based on morphological descriptions of mature stomata is largely artificial: the genesis of "paracytic" stomata, for example, may involve as few as two or as many as eight cell divisions. Tomlinson (1974; see also Dahlgren & Clifford, 1982) proposed a new classification of stomata based on developmental sequences, but unfortunately no aroids have yet been studied from this viewpoint.

Hydathodes occur in many hygrophilous Araceae, especially Philodendroideae, Colocasioideae, and Aroideae, at the attenuated "drip-tips" of leaves, either singly or in large groups (Müller, 1919; Engler, 1920b; Solereder & Meyer, 1928). Müller (1919) recognized three types in Araceae (see Table 2) but did not adequately document the distribution of these within the family. Her "*Philodendron* type" hydathodes, which differ only slightly from normal stomata, are the most widespread and probably should be regarded as the most primitive.

Most aroid roots possess a simple (one-cell-layer-thick) epidermis; however, two epidermal layers are said to occur in roots of *Amorphophallus*, *Schismatoglottis*, *Aglaonema*, *Dieffenbachia*, and other genera, three in *Stylochaeton*, four in *Zamioculcas*, and up to six in *Anthurium* and *Homalomena* (Lierau, 1888; Solereder & Meyer, 1928). The multilayered epidermis of aerial roots in some epiphytic *Anthurium* species may become secondarily thickened, nonliving, and capable of absorbing water. This is the only clear case in Araceae wherein a true velamen occurs, of the type found in many Orchidaceae (Lierau, 1888; Solereder & Meyer, 1928; Dahlgren & Clifford, 1982; French, in press).

The outermost (or single) epidermal layer forms the root hairs, which are usually simple but may be forked or branched, especially in certain aerial roots (Lierau, 1888; Solereder & Meyer, 1928). Certain taxa, such as Calloideae (Krause, 1908), appear to lack root hairs, probably accounting for Cronquist's (1981) incorrect generalization of Araceae as "mycorrhizal, without root hairs." Two basic types of root hair development are known in Araceae (Leavitt, 1904; see also Dahlgren & Clifford, 1982; French, in press): Type I, observed in *Aglaonema*, *Dieffenbachia*, *Zantedeschia*, *Caladium*, and *Arisaema*, is characterized by the ability of any protodermal cell to form a root hair; in Type II (*Monstera*, *Anthurium*) only specialized cells can form root hairs. This intriguing distribution suggests that Type II root hairs, being associated with phenetically more primitive genera, are primitive in Araceae. A more extensive inventory is highly desirable.

Vascular anatomy. Many modern general texts (e.g., Dahlgren & Clifford, 1982) perpetuate the notion, based on the very incomplete survey of Cheadle (1942), that Araceae lack vessels in the stem. Although this is true of most genera, vessels have now been reported from stems of several vining Araceae, including species of *Pothos* (Solereder & Meyer, 1928; Hotta, 1971), *Epipremnum*, *Rhaphidophora*, *Scindapsus* (Hotta, 1971), and *Philodendron scandens* (French, in press). Vessels of Araceae are primitive, with scalariform perforation plates, and apparently rather difficult to distinguish from the large, specialized "vessel-form tracheids" (Hotta, 1971).

According to Cheadle's theory (see, e.g., Cheadle & Tucker, 1961), the specialization of vessels was unidirectional, beginning in the roots. If true, this evidently implies that the vining growth habit in Araceae is derived, since vessels of the stem occur only in climbers (cf. Hotta, 1971).

Vascular bundles are more or less scattered in aroid stems, as is typical for monocots (Cronquist, 1981), although the majority tend to be concentrated centrally. The course of leaf traces in the cortex, a subject apparently without taxonomic importance, is discussed by French (in press). More significant is the occasional presence of an independent, permanent cortical vascular system, which has been observed in numerous Araceae (see Table 2), including many Pothoideae and all genera of the tribe Monstereae (Solereder & Meyer, 1928; French & Tomlinson, 1980, 1981a–d, 1984). French & Tomlinson (1983) reported that permanent cortical vascular systems are characteristic of New World Colocasioideae but are absent in the Old World genera (with the possible exception of *Hapaline*; see French, in press).

Vascular bundles in Araceae are of four different types: simple collateral bundles, compound bundles, amphivasal bundles, and compound/amphivasal transitional forms. The characteristics and

distribution of these types were summarized by French & Tomlinson (1986) and French (in press), who pointed out that the four categories intergrade. Collateral bundles occur mainly in scandent species and species with perfect flowers; they are probably the primitive type. Amphivasal bundles predominate in Araceae with unisexual flowers. Compound bundles, which may occur with collateral bundles, are apparently restricted to *Zamioculcas*, *Rhodospatha*, *Stenospermation*, *Cercestis*, *Montrichardia*, *Philodendron*, and *Dieffenbachia* (although Solereder & Meyer, 1928, reported them from numerous other genera).

The course of vascular bundles in aroid stems was studied cinematographically by French & Tomlinson (1980, 1981a–d, 1983, 1984), whose results were summarized by French (in press). Four "artificial" categories are recognized, one of which (Pattern 2) is very widespread and perhaps primitive; the other three are restricted to Pothoideae, Monsteroideae, and a few genera here included in Philodendroideae. The same authors simultaneously studied bud trace organization in Araceae, and French (in press) has summarized these findings as well. Three major patterns have been distinguished, but their largely erratic distributions are not easily amenable to broad phylogenetic interpretation, though the information may be valuable in specific cases.

Phloem sieve-tube plastids in Araceae are of the "P"-type, as in all known monocots (Behnke, 1981). Phloem (P–) proteins are general in Araceae, as in most monocots (Behnke, 1981). It is important to note, however, that only six aroid genera in three subfamilies have been investigated with regard to these phloem characters.

Araceous stems are not known to exhibit secondary growth.

Vessels are not known to occur in aroid leaves. The most taxonomically emphasized feature of the vascular system of aroid leaves is the venation. The definitive study of aroid leaf venation is that of Ertl (1932). Hotta (1971) also studied leaf venation and apparently endorsed most of Ertl's conclusions, as follows: although venation types in Araceae vary greatly, and the extremes may appear very different, the pattern of primary venation is the same for all; there are no sharp boundaries between the more distinctive forms, and transitional forms are of regular occurrence.

Ertl (1932) concurred with Engler's (1920b) earlier conclusion that leaf venation has no decisive systematic significance. Nevertheless, the following observations of Ertl are of interest: he divided the Araceae into two major groups on the basis of leaf venation. To Group I, with essentially parallel or curved venation, belong *Gymnostachys*, all of Engler's Philodendroideae, Calloideae, and Monsteroideae, plus *Cryptocoryne* and *Ambrosina* of the Aroideae; the Colocasioideae, with a distinctive venation type of their own, are connected with Philodendroideae and Monsteroideae by transitional forms.

Group II, with essentially reticulate, dicotyledonlike venation, includes most of the Pothoideae, Lasioideae, Aroideae, and *Pistia*. *Ariopsis* of Engler's Colocasioideae seems most closely related to this group. *Pothos*, via subg. *Pothos*, appears to be transitional between the two major groups. Seedlings of most species in Group II have parallel venation typical of adult leaves of Group I (Hotta, 1971), emphasizing the unity within the family.

The more overtly parallel type of venation, basic to monocots, is probably primitive in Araceae. According to Ertl (1932), the Araceae all belong among those plants with a basically parallel or pinnate-parallel arrangement of vascular bundles in the leaves. Although superficially similar, the "reticulate"-veined leaves of certain Araceae differ fundamentally from those of dicots in that the primary vascular bundles never break down into a network, but rather pass independently to the margin or the leaf apex (Ertl, 1932); the reticulate pattern is determined not by the major veins, but by the minor ones. This notion was recently reaffirmed by Krishnamurthi & Geetha (1986); on the other hand, Inamdar et al. (1983) asserted that leaves of several monocot species studied by them (including *Colocasia esculenta*, *Epipremnum aureum*, and *Pistia stratiotes*) "show reticulate venation typical of dicotyledons."

Leaf venation patterns are accorded great, sometimes even exclusive, emphasis by leading contemporary aroid phylogenists. The taxonomic significance of these patterns is so dubious, however, and their interpretation so subjective, that it would probably be better to ignore this character altogether. When authorities cannot even agree on venation differences distinguishing the angiosperm subclasses, it seems pointless to attempt to apply this character at lower taxonomic levels.

Roots of most aroids apparently have vessels, although *Caladium* and *Pistia* may be completely vesselless (see French, in press). Aroid vessels are always of the type with scalariform perforation plates (see Dahlgren & Clifford, 1982). The stele of aroid roots is of the typical polyarch monocot type in nearly all cases, with xylem and phloem

alternating with one another (Lierau, 1888; Engler, 1905). See French (in press) for additional details.

Among aerial roots, the central cylinder occupies a larger portion of the cross section in feeder than in anchor roots and possesses broader vessels and sieve-cells. Moreover, anchor roots contain more mechanical tissue (Engler & Krause, 1908; Solereder & Meyer, 1928). Branch roots in Araceae originate opposite the xylem, as in most monocots (Dahlgren & Clifford, 1982; French, in press). There is never any secondary growth.

Ground tissues: general organization. The organization of the ground tissue in aroid stems, leaves, and roots has been discussed in detail by Grayum (1984) and French (in press). Only the most basic and phylogenetically significant features will be repeated here.

Stems of Araceae only rarely contain pith, as in *Gonatopus* (French, in press). The sclerenchymatous sheath of the outermost vascular bundles in aroid stems is sometimes fused into a ring (Solereder & Meyer, 1928). In other species, a continuous or interrupted ring of collenchyma is present in the outer cortex of the stem or petiole; this situation is known only in *Homalomena, Schismatoglottis, Philodendron, Aglaonema, Dieffenbachia,* and *Zantedeschia* of the Philodendroideae, plus *Asterostigma* and *Spathantheum* of Engler's Aroideae (Engler, 1920b).

Each vascular bundle may or may not be accompanied by groups of fibers (see Grayum, 1984, for a listing); in the peduncle and petioles of *Peltandra, Typhonodorum,* many Colocasioideae, and most Old World Aroideae, the bundles are accompanied by a collenchymatous sheath (Solereder & Meyer, 1928).

A typical endodermis has been found in the aboveground axes or subterranean stems of most Araceae (Engler & Krause, 1908; Solereder & Meyer, 1928; French & Tomlinson, 1980, 1981a–d, 1983, 1984; see Table 2). A very unusual type of endodermis, in which the vascular bundles are surrounded individually, is reported in stems of Schismatoglottidinae, plus *Peltandra* and *Typhonodorum* (French & Tomlinson, 1981d; French, in press).

A sclerotic or thin-walled hypodermis may occasionally be present, as in the stems of *Cercestis* (French & Tomlinson, 1981c) and the tubers of *Colocasia fallax* (French & Tomlinson, 1983).

Typical aroid leaves have a bifacial mesophyll, with the spongy layer accounting for the majority of the thickness (Solereder & Meyer, 1928). Truly centric mesophyll structure is found only in *Typhonodorum* (Dalitzsch, 1886). The cells of the palisade mesophyll in Araceae are generally short and broad, and most often in a single layer (Dalitzsch, 1886). The cells of the spongy mesophyll have a very characteristic, mostly four-rayed, stellate form (Dalitzsch, 1886). See French (in press) for additional details.

In leaves of some species of *Anthurium, Philodendron,* and *Caladium* there is a chlorophyll-free hypodermis of one or more cell layers, directly under the epidermis of one or both sides (Dalitzsch, 1886).

The pith of aroid roots is initially of thin-walled cells, but these may become variously thickened in many genera (Solereder & Meyer, 1928). French (in press) provided a lengthy account of root cortex organization in Araceae. In all investigated aroids, the innermost cells of the cortex form a typical endodermis with Casparian strips, at least in young roots (Solereder & Meyer, 1928). The outermost layer of the cortex may form a one-cell-layer-thick (at least in Monsteroideae), suberized exodermis, particularly in species with a velamen or multilayered epidermis. Though not universally present, an exodermis has been reported from a wide range of species (see Solereder & Meyer, 1928). A small-celled, sclerenchymatous hypodermis develops beneath the exodermis in roots of *Culcasia, Cercestis, Furtadoa, Homalomena,* and *Philodendron* (French, 1987a); Shishkoff (1987) reported a "dimorphic hypodermis" from a variety of aroid genera, clearly referring to the tissue here termed "exodermis." Cork formation is known in aerial roots of *Anthurium,* several Monstereae, and *Philodendron,* following the appearance of a cork cambium (phellogen) below the exo- or hypodermis (see French, in press). Secondary wall thickening can occur anywhere in the cortex of aroid roots, least frequently in the outermost layers.

Ground tissue: universal features. Engler (1920b) placed great importance on two features of aroid ground tissue: the presence or absence of trichosclereids (distinctively branched sclereid cells), and the presence or absence and structure of tanniniferous cells and "laticifers." He regarded these features as having the distinct advantage of being universal: they are, with few exceptions, consistent within a given species, regardless of the organ examined or the age of the plant (Engler, 1920b).

Trichosclereids are characterized by their elongate shape and regularly branching development (Nicolson, 1959, 1960b). Among monocots, they

TABLE 2. Vegetative anatomy of Araceae. Summary of important characters.

Subfamily, genus	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Pothoideae											
Gymnostachys	I				—	—	—	—#	—		
Pothos	IIdT	H			—	+	+	(+)	—	—	+
Pedicellarum											
Pothoidium					—	+		+		—	+
Zamioculcas	II	H	P		—	—	—	—#	—	—	—
Gonatopus	II	H			—	—	—	—#	—		
Anadendrum					—	—	—	—#	—		
Anthurium	II	H	T	P	—	+, —	+	—#	C	+	(+)
Spathiphyllum	I	H	P		*	—	+	+	C	—	—
Holochlamys					—	—	—	+	—		
Heteropsis					—	+	—	—#	—		
Rhaphidophora	Id	AhH	TP	P	—	+	+	+	C	—	(+)
Monstera	Id	H	T	P	—	+	+	+	—	—	(+)
Amydrium					—	+	+	—#	—		
Epipremnum		H	T	P	—	+		+	C	—	*
Scindapsus			T		—	+	+	+	—	—	(+)
Alloschemone					—	+		+			
Stenospermation	I			A	+	+		+	C	—	—
Rhodospatha					+	+		+	C	—	—
Lasioideae											
Orontium	I	E	A		—	—	+	—	F	+	
Lysichiton	I		A		—	—	—	—	C		
Symplocarpus	I	Ah	A			—	+	—	C	+	
Stylochaeton					+	—	—	—	C		
Cyrtosperma	II				—	—	—	—	C?[3]		
Lasia	II			P	—		—	—	C?		
Anaphyllum								—	C?		
Podolasia								—	C?		
Urospatha					—	—	—	—	C?		
Dracontioides					—	—	—	—	C?		
Dracontium								—	C?		
Pycnospatha											
Philodendroideae[1]											
Calla	I	Ah		P	*	—	—	—	C?		
Furtadoa									F		
Homalomena		AhH			*	—	—	—#	F	+	—
Aglaonema	I			A	*	—	—	—	F	+	
Aglaodorum					—	—	–	—	F		
Zantedeschia	I	Ah		PA	—	—	—	—	F	+	
Anubias		H			—	—	—	—	F		
Schismatoglottis		AhH	T	P	—	—	(+i)	—#	F	+	—
Piptospatha					—	—	+i	—	F		
Bucephalandra					—	—	+i	—	F		
Phymatarum					—	—	+i		F		
Aridarum					—	—	+i	?	F		
Heteroaridarum											
Hottarum					—	—	+i		F		
Typhonodorum	I	Ah			—	—	+i	—	F		
Peltandra	I	H			—	—	+i	—	F	+	
Philodendron	I	H	T	P	*	+	—	—#	F	+	(+)
Dieffenbachia			T	A	+	+	—	—#	F	+	—

TABLE 2. Continued.

Subfamily, genus	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Bognera											
Carlephyton									F		
Colletogyne									F		
Arophyton									F		
Mangonia											
Asterostigma								—	F		
Synandrospadix								—	F		
Taccarum								—	F		
Gorgonidium								—	F		
Gearum								—			
Spathantheum								—			
Spathicarpa		II			A		—		—#	F	*	—
Cercestis						—	—	—	—#	F	+	—
Culcasia			H		A	—	—		—#	—		
Nephthytis						—	—	—	—#	F	+	—
Anchomanes		II							—	F		
Pseudohydrosme									—			
Montrichardia			Ah			+	—	—	*	F	(+)	—
Callopsis							—	—	—	F		
Filarum												
Ulearum									—			
Zomicarpella									—	T		
Colocasioideae												
Zomicarpa			H						—	T	+	
Jasarum							—	—	—	T		
Scaphispatha									—	T		
Caladium		Id	H	P	A		+	—	—#	T	+	—
Aphyllarum									—			
Xanthosoma		Id	Ah	P	A		+	—	—#	T		
Chlorospatha							+	—	—	T		
Syngonium		Id	H	P	P	+	+	—	—#	T	+	—
Hapaline							—	—	—	T		
Steudnera					C		—	—	—#	T		
Colocasia		Id	Ah	P	C		—	—	—#	T	+	
Gonatanthus									—#	T		
Remusatia							—	—	—#	T	+	—
Alocasia		Id	Ah	P	A	+	—	—	—#	T	+	
Protarum									—	T		
Aroideae												
Arum		II	Ah		P	+			—	F	+	
Dracunculus						+			—	F		
Helicodiceros		II							—	F		
Theriophonum									—	F		
Typhonium		II	Ah	P					—	F		
Sauromatum		II			P				—	F		
Eminium									—			
Biarum									—	F	+	
Arisaema		II	H	P(A?)					—			
Ariopsis		IId			C		—	—	—	F	+	
Pinellia		II	H			+			—	F		
Pseudodracontium									—	F		
Amorphophallus		II	H	P	P				—#	F	—	—

TABLE 2. Continued.

Subfamily, genus	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Arisarum		Ah						—	F		
Ambrosina	I							—	F		
Cryptocoryne	I					—	+—	—	C?[3]		
Lagenandra						—	—	—	C?		
Pistia	II	Ae	A		+		+	—#	C?[3]	+	

KEY

General: ( )—in some species
*—conflicting information from different sources

(I) Venation type:
II—Group II (reticulate)
I—Group I (parallel)
T—transitional
d—derived (from group indicated)

(II) Distribution of stomates:
A—amphistomatic:
e—tendency to epistomatic
h—tendency to hypostomatic
H—hypostomatic
E—epistomatic

(III) Stomate type:
P—paracytic
T—tetracytic
A—anomocytic

(IV) Hydathode type:
P—*Philodendron*-type
A—*Alocasia*-type
C—*Colocasia*-type

(V) Compound vascular bundles:
+—present
— —absent

(VI) Cortical vascular system: +—present
— —absent

(VII) Stem endodermis: +—present:
i—individual type
— —absent

(VIII) Trichosclereids: +—present
— —absent
#—substantiated negative reports (rest based on general statements)

(IX) Secretion vessels:[2]
— —completely lacking
C—single cells (idioblasts)
F—secretion files
T—secretion tubes

(X) Biforines:
+—present
— —absent

(XI) Prisms:
+—present
— —absent

[1] Properly Calloideae if used sensu this paper, i.e., to include *Calla* (see Nicolson, 1984b).
[2] Data mainly from French (1988).
[3] For Lasioideae and a few other groups, French (1988) recorded that laticifers were lacking, but did not comment on whether or not secretion cells were present.

are apparently unique to Araceae, although Gaudet (1960) described and illustrated what can only be called trichosclereids in the dicot genus *Nymphaea*; as such, they must be considered a derived character, as Nicolson (1959) concluded.

The distribution of trichosclereids within the Araceae is almost congruent with the subfamily Monsteroideae, in which all genera and species investigated possess trichosclereids in varying abundance, though not always in all organs. They are absent, for example, from the leaves of *Epipremnum* (Nicolson, 1959) and from the roots of *Rhodospatha* and *Stenospermation* (Engler & Krause, 1908), and known only from the flowers in *Amydrium* (Carvell, 1989). In both genera of the tribe Spathiphylleae, trichosclereids are longer and narrower than in Monstereae and occur in much larger groups (Nicolson, 1959, 1960b; French, in press).

Outside Engler's Monsteroideae, trichosclereids are well documented only in a few species of *Pothos* (Nicolson, 1959, 1960b; Hotta, 1971) and in *Pothoidium* (French & Tomlinson, 1981b). Solereder & Meyer (1928) reported trichosclereids in both species of *Montrichardia*, but Nicolson (1959) was unable to confirm this.

The complex subject of "laticifers" and other secretory tissues in Araceae was carefully treated by Solereder & Meyer (1928). They pointed out that the contents of aroid "laticifers" are frequently tanniniferous (i.e., not true latex) and are not well characterized for most species. They therefore employed the noncommital terms "secretion cells," "secretion files," and "secretion tubes" (in as-

cending order of specialization) for the three grades of "secretion vessels" found in Araceae. Their terminology is adopted in this paper, the second two types being grouped, for convenience, under the heading "laticifer."

Individual secretion cells occur in the ground tissue of most organs, where they are distinctive mainly due to their mostly colorless contents (Solereder & Meyer, 1928). Individual secretion cells are widespread in Araceae since species exhibiting the more specialized types of secretion vessels usually also possess all of the more generalized types. The Pothoideae and Monsteroideae, however, possess only secretion cells, or, depending on the genus, appear to lack secretion vessels altogether (see Table 2). Among the remaining aroid subfamilies, only *Symplocarpus*, *Lysichiton* (Rosendahl, 1911), *Stylochaeton* (Solereder & Meyer, 1928), the tribe Lasieae, the subtribe Cryptocoryninae, and *Pistia* are known to possess solely individual secretion cells (French, 1988).

All so-called "laticifers" in Araceae are of the articulated type, as in all other monocots (Metcalfe, 1967) with the apparent exception of *Cyclanthus* (Wilder & Harris, 1982). Secretion files are linear series of secretion cells separated from one another by cell walls (Solereder & Meyer, 1928). Their contents may be colorless (*Calla*), brown (*Zantedeschia*), or milky (*Dieffenbachia*). They occur in association with vascular bundles, although in roots they may also occur in the cortex (some *Philodendron*; New World but not Old World Colocasioideae) (Lierau, 1888).

The possession of laticifers is here interpreted as derived, since it is strongly correlated with the monoecious condition in Araceae. Among hermaphroditic aroids, only *Orontium* and *Calla* are laticiferous (French, 1988).

Secretion files, or nonanastomosing laticifers, occur widely in Calloideae, monoecious Lasioideae, Philodendroideae, and Aroideae, as well as in *Ariopsis* of the Colocasioideae (Solereder & Meyer, 1928; French, 1988).

Secretion tubes, or anastomosing laticifers, are characterized by cellular fusion and extensive and sometimes multiple branching, resulting in the formation of complicated net- or latticeworks. Fusion may occur along the longitudinal cell walls of adjacent tubes, or along the walls of abutting branch ends (Solereder & Meyer, 1928). Secretion tubes are mostly associated with vascular bundles, though they may also occur throughout the ground tissue, even in the vicinity of the epidermis.

Secretion tubes are found only in the Colocasioideae (with the exception of *Ariopsis*), including *Scaphispatha*, *Protarum*, and *Zomicarpa*, (French, 1988), all of Engler's Aroideae but here included in Colocasioideae. They appear to be limited to the aboveground organs (Lierau, 1888). The contents of secretion tubes are generally milky in New World genera but reddish in Old World tribes (pers. obs.; also noted by Trécul, 1866).

Intercellular secretion vessels—secretion spaces or secretion ducts—occur in various organs of certain aroid genera. They are typically schizogenous in origin and surrounded by an epithelium of one to several cell layers (Solereder & Meyer, 1928). "Resin" canals are generally lacking in aroid roots, except for the genera *Culcasia*, *Cercestis*, *Furtadoa*, *Homalomena*, and *Philodendron* (French, 1987b). In *Philodendron*, resinlike secretions from such ducts along the inner surface of the spathe appear to play an important role in pollination (von Martius, 1831; Warming, 1883; Schrottky, 1910; Pohl, 1931; Gottsberger & Amaral, 1984; Mayo, 1986).

Schizogenous or lysigenous mucilage canals are known only from Pothoideae, Monsteroideae, Colocasioideae (Old and New World genera), and genera here included in the Philodendroideae (see French, in press).

Calcium oxalate crystals occur in every genus of Araceae yet investigated (Nicolson, 1959). Crystal morphology varies considerably, and the distribution of various types within the family is of some taxonomic significance. For detailed reviews see Solereder & Meyer (1928), Nicolson (1959), Grayum (1984), and French (in press).

Nicolson (1959) recognized four types of calcium oxalate crystals in Araceae. The most characteristic and well known of these, in Araceae as well as monocots in general, are raphides. These are elongate, needlelike crystals occurring in bundles. They are found in the ground tissue of all vegetative organs, and rarely even in the epidermis, mostly in idioblastic cells of varying morphology. Raphides probably occur in every genus of Araceae (Nicolson, 1959). Certain features such as the length and arrangement of the crystals, the shape of the cells that contain them, and the nature of the cell wall vary intergenerically and probably have systematic value (Solereder & Meyer, 1928); however, too few data are presently available.

A very specialized type of raphide cell of particular systematic value is the "biforine." In contrast to typical raphide cells, with which they may occur, biforines are rather thick walled, except that at each end there is a thin-walled spot, which is generally narrower than the raphide-bundle. Biforine cells are either broadly rounded at the ends or are fusiform with acuminate or papillate ends (Solereder & Meyer, 1928). Several authors have

ascribed a "blowgun" (defensive) function to these specialized cells (Hegnauer, 1963; Tchiakpè, 1979; Middendorf, 1983; French, in press).

According to Nicolson (1959), biforines are characteristic of subfamilies with unisexual flowers and do not occur in either Pothoideae or Monsteroideae. Solereder & Meyer (1928), however, also reported biforines from *Anthurium*, *Orontium*, and *Symplocarpus*, none of which were investigated by Nicolson. More data on this cell type are desirable.

So-called "styloids" (Nicolson, 1959) represent the second main type of calcium oxalate crystal in Araceae. These are reported to be very restricted in Araceae, occurring only in the two genera of the tribe Zamioculcadeae. It is unclear, however, exactly how styloids differ from typical raphides (see detailed discussion in Grayum, 1984).

The third of Nicolson's main crystal types is the druse. These are "spherical, aggregated crystals of calcium oxalate with many sharp points, resembling the spiked head of the medieval mace" (Nicolson, 1959). Druses occur in virtually all araceous genera and in all organs, usually in ground tissue but sometimes also epidermally (Solereder & Meyer, 1928). Nicolson (1959) did not regard them to be of systematic value.

The fourth main type, termed "prisms," are mostly large, solitary crystals in the form of flattened rhombohedrons (Nicolson, 1959). Nicolson (1959) reported these only from Potheae and Monsteroideae; they are occasional in the latter tribe and are characteristic of the former, where they are generally found in cells along vascular strands. Solereder & Meyer (1928) reported crystals of this description also from single species of *Anthurium* and *Philodendron*.

"Crystal sand," consisting of minute crystals held by Nicolson (1959) to be of unknown composition, was reported from every aroid genus examined and is hence considered of no systematic significance (Nicolson, 1959). Franceschi & Horner (1980) regarded crystal sand as a form of calcium oxalate.

FLORAL MORPHOLOGY AND ANATOMY

General considerations. Aroid inflorescence and floral morphology have recently been exhaustively reviewed by Grayum (1984), and some pertinent details appear in Bogner (1987) and Grayum (in press b). The phylogenetically significant aspects of this field are discussed below, and some more salient features are summarized in Table 3.

The aroid inflorescence is virtually without exception a spadix (an unbranched, fleshy axis bearing crowded, sessile flowers) subtended by a single, mostly rather large bract, the spathe. It is always morphologically terminal (Ray, 1988), in contrast to Cyclanthaceae where axillary inflorescences are most common and considered primitive (Wilder, 1988). The general structure of the inflorescence is one of the most consistent and characteristic features of the Araceae. Deviations from the basic plan are rare, and such reports are sometimes rather dubious.

The spathe. The ultimate bractlike or leaflike structure below the spadix is ordinarily designated as the spathe. Only in *Gymnostachys* and *Orontium* is a spathe regularly lacking, according to Ray's (1988) interpretations. In these genera the ultimate foliar organ is designated as a mesobracteole or sympodial leaf, respectively. In *Pothoidium*, the spathe appears to be lacking in the uppermost inflorescences, which are enclosed when young by the foliage leaves of the main stem (Engler, 1877).

The absence of a spathe in genera such as *Gymnostachys* and *Orontium* may represent the primitive condition in Araceae; these genera, however, exhibit many autapomorphic character states, and it is equally likely that the spathe has been secondarily lost.

The variation in gross morphology of the spathe within Araceae is extreme. The highly differentiated and specialized spathes of genera such as *Gonatanthus* or *Cryptocoryne* bear about the same relationship to the simple, bractlike spathes of *Pothos* or many *Anthurium* species as does a pitcher leaf of *Sarracenia* or *Nepenthes* to an unspecialized dicot foliage leaf. Most modifications of the spathe are closely correlated with pollination biology and the distribution of male and female flowers on the spadix.

The classifications of spathe and spadix types that follow are more or less original, but compare also the systems of Engler (1884, 1920b) and Goebel (1931).

The simplest types of spathes (Type I; see Table 3) appear to have only the function of enclosing and protecting the spadix in bud. Such spathes are often green or otherwise inconspicuously colored and probably play little if any role in pollination. Type I spathes are mostly found in genera with bisexual flowers, especially in Engler's Pothoideae, but are also known from certain genera with unisexual flowers (some Spathicarpeae and Zomicarpeae).

The next stage of specialization, Type II spathes,

TABLE 3. Floral morphology of Araceae. Summary of important characters.

Subfamily, genus	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Pothoideae											
Gymnostachys	I	H	+4	L4	L		1	1	Ap	O	+
Pothos	I	H	+6	L6	L		3	1	Ab, Ac	A	—
Pedicellarum	I	H	+6(F?)	L6	L		3	1	Ab?	A	—
Pothoidium	I	H	+6	L(3)6	L	3–6	1	1	Pb1	A	—
Zamioculcas	IV	MIIIb	+4	L4	L	0	2	1	Ac	Ams	+
Gonatopus	IV	MII	+4	L4F	Ap	0	2	1	Ac	A	+
Anadendrum	I	H	+F	L4	L		1	1	B	A	—
Anthurium	I, II	H	+4	L4	L		2	2	Ac	A(Cs)	+
Spathiphyllum	II	H	+(4)6(8)(F)	L(4)6(8)	L		(2)3(4)	(1–4)6–8	At, Ab, Ac	A	+
Holochlamys	III	H	+4F	L4	L		1	∞	Ba	A	+
Heteropsis	II	H	—	L4	Al		1	4	Pb*2	A	—
Rhaphidophora	II	H	—	L4	L		1	∞	Pt*2–3	A	+
Monstera	II	H	—	L4	L		2	2	Ab	A	—
Amydrium	II	H	—	L4	L		1	2	Pc 1–2	A	—
Epipremnum	II	H	—	L4	L		1	2–4(6)	Pt, Pb1	A	+
Scindapsus	II	H	—	L4	L		1	1	B	A, Am	—
Alloschemone	II	H	—	L(?)	L		1	1	B	Am	?
Stenospermation	II	H	—	L4	L		1–2	4+	Ab, Pb*2	A	+
Rhodospatha	II	H	—	L4	L		2	∞	A+	Am(A)	T
Lasioideae											
Orontium	I	H	+6	L6	L		1	1	B	Ah	—
Lysichiton	II	H	+4	L4	L		2	1–2	Ac	O	—
Symplocarpus	III	H	+4	L4	L		1	1	Ap	O	—
Stylochaeton	IV	MII, MIIIb	+F	L4–6	L L	0	1–4	1–2–∞	Pt, b2–4, Ac	A, Ah	+
Cyrtosperma	II	H	+6(4–5)	L6(4–5)	L		1	∞(1–2)	Pb, Pc1	A	T
Lasia	II	H	+4(6)	L4(6)	L		1	1	Pap1	A	—
Anaphyllum	II	H	+4	L4	Al		1	1	Pc1	A	—
Podolasia	I	H	+4, 6	L4, 6	L		1	1	Pb1	A	—
Urospatha	III	H	+4, 6	L4, 6	Al		2	2+	Ac	A	—
Dracontioides	III	H	+4–5	L4(7–9)	Al		(1)2	1(2)	Ab, Pb1	A	T
Dracontium	III	H	+4–8	L4, 6(9–12)	Al		2–5	1	Ac, Ab	A; Cs	T
Pycnospatha	III	H	—	L"several"	Al		1	1	Pb?	A(h)	T

TABLE 3. Continued.

Subfamily, genus	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Philodendroideae[1]											
Calla	II	H	—	L10–12	L		1	6–9	Ba	A	+
Furtadoa	III	MIIIb	—	Bp1	Ap	2(?)	1	∞	B	Ah	?
Homalomena	III, IV	MIIIb(MII)	—	Bp2–4(5–6)	L, A1, Ap, T	(0)1(2–3)	(1)2–4(5)	4–∞	Pt, Pb*2–4 (Ab)	A, Ah	+
Aglaonema	III(f)	MII	—	Ba1(2?)	Ap	(very rare)	1(2)	1	B	A, Ah	—
Aglaodorum	III	MIIIb	—	Ba3–4	Ap	1–3	2	1	Pc	A	?
Zantedeschia	III	MII	—	B(p?)2–3	Ap	0(3)	1–5	4	At, Ab, B	A	+
Anubias	III, IV	MII, MIIIb	—	Bp(2)3F	L	0	2–3	∞	At, Ab, Pb	A(h)	+
Schismatoglottis	III, IV	MIIIa (b, c)	—	L2–3(F)	Ap	(1–4)	1	∞(1)	Pt(Pb) 2–4	A(h), O	+
Piptospatha	III	MII, MIIIb, c	—	Ba1–2?	Ap	0	1	∞	Pt, Pc 2–3	Ah; Os	
Bucephalandra	III	MIIIc	—	Ba1	Aph	0	1	∞	B	O	?
Phymatarum	IV	MIIIc	—	Ba1	Aph	0	1	15–25	B	O	+
Aridarum	III	MII, MIIIa–c	—	Ba1–2f	Aph	0	1	∞	B	O	+
Heteroaridarum	IV	MIIIc	—	Ba2–3f	Aph	0	1	∞	ApB	O	+
Hottarum	III, IVf	MIIIa–c	—	Ba2–3f	At, Ap	0	1	12–15	B	O(s)	?
Typhonodorum	IV	MIIIc	—	Bp4–8F	A1	3–6	1	1–2	Pb3–6	O	—
Peltandra	IV	MIIIc	—	Bp4–5F	Ap	4–5F	1	1–few	Pc, B	O(h)	T
Philodendron	IV	MIIIb(MIIIc)	—	Bp2–6	Ap	(very rare)	(2–3)4–6 (7–47)	(1)–4–∞	At, Ab, Ac, (B)	O, Ah	+
Dieffenbachia	IVf	MIIIb	—	Bp4–5F	A1, Ap	4–5	2–3	1	Ab	A, Ah	—
Bognera	IIIf	MIIIb	—	Bp3–4F	Al	0	1	1	B	A?	?
Carlephyton	IIIf	MI, MIIIa	—	Bp, L(1) 2–6F	L	3–4F	1	1	B	O	—
Colletogyne	IIIf	MII	—	L1	L	F	1	1	B	O	—
Arophyton	IVf	MIIIa, b, c	—	Bp2–5F	L, A1, Ap	F	1	1	B	O	—
Mangonia	III	MIIIa	—	L3–5F	Ap	3	2–3	2	Ac	A	?
Asterostigma	III(f)	MI	—	Bp3–4F	At	3–5(F)	3–5	1	Ab	Ah	+
Synandrospadix	IIf	MI	—	L4(5–6)F	L	3–5	3(5)	1	Ab	O	+
Taccarum	III	MI	—	L4–8F	Ap	4–6	3–6	1	Ac	A	?
Gorgonidium	III	MI	—	L4(6–8)f	Ap	6–8	4	1	Ab	O	?
Gearum	III	MII	—	Bp(?)4(5?)	Ap	+	3–4	1	Ab	?	+
Spathantheum	IF	MDv	—	L4–7F	L	5–8	6–8	1	Ab	Os	?

TABLE 3. Continued.

Subfamily, genus	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Spathicarpa	IF	MDv	—	L3–4F	A1	3	1	1	Ba	O	+
Cercestis	III	MII, MIIIb	—	Bp2–4	Ap	0	1	1	B, Pb1	A, Ah	—
Culcasia	III, IV	MIIIb, MII	—	Bp3–4	Ap	0	1–3	1	Ab, B	A, Ah	+
Nephthytis	II	MII	—	B(a?)2–4	Ap	0	1	1	B	A	—
Anchomanes	III	MII	—	B(a?)2	Ap	0	1	1	Pb1	A	—
Pseudohydrosme	III	MII, MIIIa	—	Bp, L 2–5(f)	Ap, L	0	2(3)	1	Ab	A	?
Montrichardia	III	MII	—	B(p?)3–6	L	0	1	1–2	Pb1	A	—
Callopsis	IIf	MII	—	Ba2–3	Ap	0	1	1	B	A	+
Filarum	If	MIIIc	—	Ba1	L	0	1	1	B	?	?
Ulearum	If	MIIIc	—	Ba2–3	Ap	0	1	1	B	A	—
Zomicarpella	I?f	MIIIa	—	B(?)	Ap	0	1	1	B	A	?
Colocasioideae											
Zomicarpa	IVf	MIIIa	—	Ba1–2	At	0	1	6	B	A	+
Jasarum	IV	MIIIb	—	Bp3–4F	Ap	0	1	2	B	Ah	—
Scaphispatha	IV	MII	—	Bp4F	Ap	0	1?	5±	B	A	+
Caladium	IV	MIIIb	—	Bp3–4(5)F	Ap	0	1–2	2–10	Pt*	A	+
Aphyllarum	IV	MIIIb	—	Bp3–4F	Ap	0	1	2	Pb*	A	+
Xanthosoma	IV	MIIIb	—	Bp4–6F	Ap	(very rare on upper flowers)	2–4	∞	At	A, Ah	+
Chlorospatha	IVf	MIIIb	—	Bp3–5F	Ap	0	(1)3–4	few–∞	At	A(h)	+
Syngonium	IV	MIIIb	—	Bp2–5F	Ap	0	(1)2(3)	1	Ac	A	—
Hapaline	IVf	MIIIc	—	Bp3F	Ap	0	1	1	Pc1	A	+
Steudnera	II	MII	—	Bp3–6F	Ap	3–5	1	∞	Pt2–5	Ah, O	+
Colocasia	IV	MIIIc	—	Bp3–6F	Ap	0	1	∞	Pt2–4	O(s)	+
Gonatanthus	IV	MIIIb	—	Bp2–3F	Ap	0	1	∞	B	O	+
Remusatia	IV	MIIIb	—	Bp2–3F	Ap	0	1	∞	Pt2–4	O	+
Alocasia	IV	MIIIc	—	Bp3–8F	Ap	0	1	few–∞	Pb	Ah, O	+
Xenophya	IV	MIIIc	—	Bp5–12F	Ap	0	1	6–10	Pb	A, Ah	+
Protarum	IV	MIIIc	—	Bp3F	?	4–6	1	4	B	O	?
Aroideae											
Arum	IV	MIIIc	—	Ba3–4	Ap	0	1	6+	Pt1	O	+
Dracunculus	IV	MIIIc	—	L3–4f	L	0	1	few (<6)	ApB	O	+

TABLE 3. Continued.

Subfamily, genus	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Helicodiceros	IV	MIIIc	—	Ba2–3	Al	0	1	few (<6)	ApB	O	?
Theriophonum	IV	MIIIc	—	Ba1–2	Ap	0	1	few–∞	ApB	O	+
Typhonium	IV	MIIIc	—	Ba1–3	Al, Ap	0	1	1–2	B	O	+
Sauromatum	IV	MIIIc	—	Ba(few)	Ap	0	1	2–4	B	O	+
Eminium	III	MIIIc	—	Ba2	Al	0	1	2	B	O	?
Biarum	III	MIIIc	—	Ba1–3	Al, L	0	1	1	B	O	+
Arisaema	III, IV	(PII)(MII) PIIIa	—	L2–5Ff	L, Al, Ap	0	1	1–2–9	B	O	+
Ariopsis	IIIf	MIIIb	—	(see text) 3F	Lp	0	1	∞	Pt4–6	O	+
Pinellia	IVf	MIIIc	—	Ba2	At	0	1	1	B	O, Ah	+
Pseudodracontium	III	MIII	—	L3–6	Al	0	1	1	B	A	?
Amorphophallus	III	MIIIa (MIIIb, c)	—	Ba1–6	(At)	(+)0	1–4	1	Ab, Ac, B	A, Ah	—
Arisarum	III	MIIIa	—	L1	T	0	1	several	B	O	+
Ambrosina	IIIf	MIIIb	—	Ba2	L	0	1	∞	B	O	+
Cryptocoryne	IV	MIIIb	—	Ba1(2)	Aph	0	1	few–∞	Pt1	O	+
Lagenandra	IV	MIIIb	—	Ba1(2)	Ap	0	1	1–6	B	O	+
Pistia	IIIf	MIIIb	—	L2F	Lp	0	1	∞	Pt2–3	O	+

KEY

(I) Spathe type:
- I—(unmodified, bractlike)
- II—(expanded and/or colored)
- III—(enclosing spadix)
- IV—(constricted)
- F—fused to spadix entire length
- f—fused to spadix in lower part

(II) Spadix type:
- H—hermaphroditic
- M—monoecious
  - I—bisexual flowers in center
  - II—male and female flowers contiguous
  - III—with sterile flowers or gap:
    - a—sterile flowers or gap above male flowers
    - b—sterile flowers or gap between male and female flowers
    - c—both of the above
  - Dv—dorsiventral segregation
- P—paradioecious (see text)

(III) Perigonium:
- +—present (number of tepals indicated)
- —absent
- F—fused

(IV) Stamens (number indicated):
- L—long
- B—broad
  - a—*Amorphophallus*-type
  - p—*Philodendron*-type
- F—fully fused into synandria
- f—fused only at base of filaments

(V) Anther dehiscence:
- L—longitudinal
  - p—pores
- T—transverse
- A—apical
  - l—longitudinal slit
  - p—pores
  - h—horns
  - t—transverse slit

(VI) Staminodia (number indicated):
- +—present (number unknown)
- 0—absent
- ?—questionable
- F—fused

(VII) Locules (number indicated)

are broadly expanded at maturity and/or brightly colored with some obvious role in attracting pollinators. This stage is most characteristic of taxa with bisexual flowers (especially *Anthurium* and the Monsteroideae) but occurs rarely in monoecious genera (*Nephthytis*, *Callopsis*, *Steudnera*).

The spathe in most monoecious aroid genera, especially in Philodendroideae and Aroideae, is somewhat funnelform to cucullate and/or tubular at maturity and wraps all around at least the lower portion of the spadix. Such a specialized type (Type III) can also be seen in a few genera with bisexual flowers, e.g., *Symplocarpus* and *Dracontium*.

The most highly specialized spathes (Type IV) more or less completely surround the spadix at maturity and are constricted in one or two places, so that a lower "tube" and an upper "lamina" may be distinguished. This is the usual condition in Colocasioideae and occurs commonly in Philodendroideae and Aroideae; it is not known from genera with bisexual flowers. The constriction may be above the inflorescence, as in *Stylochaeton* and the Cryptocoryninae; between the sterile appendix and the male portion of the spadix, as in *Zomicarpa*, *Arisaema*, at least some *Alocasia* species (pers. obs.) and most Arinae; or between the male and female portions of the inflorescence, as in most other genera. In *Gonatanthus*, there are two constrictions: one between the male and female portions of the spadix and a more pronounced one above the entire inflorescence (Engler & Krause, 1920).

Constrictions of the aroid spathe are known to play important roles in pollination biology (see, e.g., Gottsberger & Amaral, 1984).

The spathe is frequently decurrent on the peduncle and in some cases is fused to the fertile part of the spadix. In the closely related genera *Spathicarpa* and *Spathantheum*, the spathe and spadix are fused over the entire length of the latter (Subtype F, Table 3). Many other monoecious genera show an intermediate stage, with fusion only in the lower fertile regions, such that all of the female flowers and occasionally even some male flowers are borne unilaterally on the spadix (Subtype f, Table 3). A tendency toward this condition, in which only the lowermost part of the female region is involved, can be seen in some species of *Philodendron*, *Caladium*, and *Alocasia*.

The spathe may persist until the fruits are mature, or it may gradually rot away. In *Anadendrum*, *Heteropsis*, and the Monstereae, the entire spathe abscises cleanly following anthesis (Engler, 1905; Engler & Krause, 1908). In other taxa, such as Schismatoglottidinae (French & Tomlin-

(VIII) Ovules/locule (number indicated):
∞—numerous

(IX) Placentation:
A—axile:
ap—ovules at apex only
b—ovules at base only
c—ovules in center only
t—ovules along whole length
Ap—apical
B—basal:
a—derived from axile
ApB—apical and basal
P—Parietal (number of placentae indicated):
*—intrusive placentae
ap—ovules at apex only
b—ovules at base
c—ovules in center
t—ovules full length

(X) Ovule type:
A—anatropous
Am—amphitropous
C—campylotropous
O—orthotropous:
s—sub-
h—hemi-
Data mainly from French (1986c)

(XI) Endosperm:
+—present
—absent
T—trace

[1] Properly Calloideae if used sensu this paper, i.e., to include *Calla* (see Nicolson, 1984b).

son, 1981d), *Chlorospatha* (pers. obs.), *Syngonium* (Croat, 1981), and *Alocasia* (Nicolson, 1968a; Burnett, 1984), only the lamina abscises and the tube persists.

The spadix. A few species of Araceae do not technically bear flowers on spadices but, rather, in spikes. The bisexual perigoniate flowers of *Pedicellarum* and some species of *Pothos* sect. *Allopothos* are rather distantly disposed on a slender, ligneous axis; male flowers of *Filarum*, *Arisarum*, and many species of *Arisaema* may also be remote from one another (Engler, 1920b; Nicolson, 1966). If the spadix is indeed derived from a spike and, ultimately, a raceme (see Stebbins, 1973), then these inflorescences must be regarded as primitive within Araceae.

In *Pedicellarum*, the flowers are supposed to be pedicellate (Hotta, 1976), which would make the inflorescence a raceme and hence potentially even more primitive. However, in the material of this genus that I have examined (*Martin & Ismawi S36660* MO), the flowers are always sessile.

Bracts supposedly never occur on the aroid spadix itself (Engler, 1884); however, Eyde et al. (1967) described "vascularized appendages" between some flowers on spadices of two *Pothos* species, and bracts may occasionally occur on the lower flowers in some *Anthurium* species (Engler, 1905). According to Engler (1884) and Burger (1977), the bractless nature of the aroid spadix suggests a bracteal origin of the perianth members.

The arrangement of individual flowers on the aroid spadix is usually spiral, although in some cases the flowers may be whorled, as in species of *Asterostigma*, *Arum*, *Biarum*, *Lagenandra*, and *Cryptocoryne*. The whorled arrangement appears to have been derived from a spiral organization (Engler, 1884; Benzing, 1969).

The number of flowers on most aroid spadices is indefinite, but there is a tendency toward reduction in some groups. The number of male flowers is reduced to 8–10 in *Ambrosina*, and to only one in *Pistia*; there are only a few female flowers in *Aglaodorum*, *Ariopsis*, *Stylochaeton*, *Zomicarpa*, *Filarum*, and *Cryptocoryne*, and just one in *Ambrosina* and *Pistia*. Inflorescences of *Pedicellarum* and some species of *Pothos* bear only a few bisexual flowers (five or fewer in the former genus).

Two sexual systems predominate in Araceae: hermaphroditism, in which each inflorescence is more or less completely covered with bisexual flowers; and monoecy, in which each inflorescence bears separate male and female flowers. In most species of *Arisaema* some plants produce only male inflorescences and others only female inflorescences during a particular season, but may produce inflorescences of the opposite sex or even (depending on the species) monoecious inflorescences in a different season (Hotta, 1971). The sexuality of a given plant is evidently correlated with such factors as age, size, and nutritional state. The situation in *Arisaema* has been referred to as "paradioecy" (Hara, 1971) or, better, as "sequential monoecy" (Bawa, 1980) or "sequential cosexuality" (Lloyd, 1979). The same condition may also occur rarely in *Cryptocoryne*, as in *C. lucens* (Jacobsen, 1976).

No Araceae are known to be truly dioecious; Engler's (1905) tentative interpretation of dioecy in *Pothoidium* was in error (J. Bogner, pers. comm.).

Unisexual flowers have clearly been derived from bisexual flowers in Araceae (Engler, 1884; Eyde et al., 1967; Hotta, 1971), as in monocots (Howarth, 1957) and angiosperms as a whole (Bawa & Beach, 1981). Thus, hermaphroditism is to be regarded as primitive, monoecy derived, and "sequential cosexuality" even more derived. One piece of evidence for this hypothesis is the distribution of male, female, and sometimes bisexual flowers on monoecious aroid inflorescences. In virtually all monoecious species the female flowers are situated on the lower part of the spadix with the male flowers above. Bisexual flowers, whenever present, occur in between. Based on the assumption that pollen would tend to fall or be carried downward by insects foraging from top to bottom on an inflorescence, Engler (1884) concluded that flowers in the lower part of a hermaphroditic spadix would on average receive more pollen and thus set more fruit than those in the upper part. Upper flowers would ultimately become masculine and lower flowers feminine, he reasoned, in Lamarckian fashion, due to "disuse" of their pistils and stamens, respectively. It is perhaps significant in this regard that spadices of many nominally hermaphroditic aroids exhibit the predicted tendencies: *Calla* (Krause, 1908; Goebel, 1931) and *Orontium* (Schaffner, 1937; Hotta, 1971) frequently produce a few male flowers toward the tips of their spadices, and *Heteropsis* (Engler, 1905) and many Monstereae (Engler & Krause, 1908) often bear some basal female flowers. Furthermore, there is a tendency even in species with uniformly bisexual flowers (e.g., many *Anthurium* species) for only the lower flowers to set fruit (Engler, 1905; pers. obs.).

The curious dorsiventrally segregated distribution of male and female flowers in *Spathicarpa* (and to a lesser extent in the closely related genus

Spathantheum) appears strikingly at variance with the usual aroid pattern. This peculiar distribution has, however, been elegantly explained by Troll (1928) and Uhlarz (1982) as a developmental consequence of the complete fusion of spathe and spadix, which likewise occurs only in these genera. The dorsiventral segregation of various flower types in some species of *Hottarum* (Bogner, 1983; Bogner & Hotta, 1983) is perhaps explicable in a similar manner.

Hermaphroditism is characteristic of Engler's subfamilies Pothoideae (except as noted in Table 3), Monsteroideae, and Calloideae, and of the tribe Lasieae of subfamily Lasioideae. All other aroids are monoecious. The arrangement of flowers on monoecious aroid inflorescences is quite variable and may involve sterile male and/or female flowers in addition to fertile male, female, and occasionally bisexual flowers. Sterile flowers may be present in various positions, often occupying a considerable portion of the spadix and sometimes playing an important auxiliary role in pollination.

Presumably the most primitive type of monoecious spadices in terms of floral distribution, if Engler's scheme is correct, retain some bisexual flowers in the middle and have not yet evolved sterile flowers. This type of spadix (Type I, Table 3) is rather infrequent in Araceae but occurs in species of *Carlephyton* (Bogner, 1972) and in several Spathicarpeae (Engler, 1920a). A slightly more advanced stage is probably represented by spadices with the male and female regions abutting directly, without evidence of bisexual or sterile flowers. This condition (Type II) occurs in most major groups (see Table 3).

Type III spadices lack bisexual flowers but bear sterile flowers, which may occur either above (Subtype IIIa) or below (Subtype IIIb) the fertile male portion of the spadix, or often in both locations (Subtype IIIc). In several genera of the Schismatoglottidinae all three subtypes are known; Hotta (1982) suggested that Types IIIa and IIIb have evolved independently from the Type II grade, and that Type IIIc might have been derived from either of the former.

Sterile flowers in Araceae are almost invariably sterile male flowers, as indicated by their position (when apical on the spadix) and/or morphology. Only in *Zamioculcas* do centrally located sterile flowers clearly represent sterile female flowers (Engler, 1905), though in several Arinae this is strongly suspected. In some other Arinae and a few species of *Amorphophallus*, central sterile flowers are so strongly modified that their sexual derivation is indeterminable.

Sterile flowers may be only slightly modified or more or less strongly modified from their fertile counterparts. Sterile male flowers of some *Asterostigma* species, for example, differ from the fertile synandria only by failing to produce pollen (Engler, 1884). Similarly, sterile male flowers in *Typhonodorum* and most Schismatoglottidinae differ little from adjacent fertile male flowers. On the other hand, sterile flowers may be highly modified as fungoid (*Pseudodracontium*), hairlike (*Amorphophallus* sect. *Dysamorphophallus* and subg. *Metandrium*, *Arisaema* sect. *Fimbriata*, various Arinae), or wartlike (*Zomicarpa*, some *Amorphophallus* species, various Arinae) structures. More often, apical sterile male flowers are strongly flattened and reduced upward, spreading apart and finally blending altogether into a smooth-surfaced to deeply rugose, bulbous, clavate, caudate or morchelloid appendage that may greatly overtop the spathe and play a major role in pollination, especially as regards heat and odor production (Knoll, 1926; Vogel, 1962). Such is the case in most species of *Amorphophallus*, *Arisaema*, and Arinae, plus *Zomicarpella* and some Arophyteae (Bogner, 1972). Only one genus in Engler's Philodendroideae (*Peltandra*) and two in Colocasioideae (*Alocasia*, *Colocasia*), possess sterile, naked apical appendages. Engler (1884) contended adamantly that such terminal appendages are elaborated from the male flowers as described above, and do not, for example, represent the prolonged central axis of the inflorescence.

The position of the central sterile flowers often corresponds to the site of the spathe constriction, when such occurs, and a role in floral biology (involving the occlusion of the spathe) has occasionally been ascribed to these as well (see, e.g., Knoll, 1926). Centrally located sterile male flowers may be differentiated morphologically from apically located ones on the same spadix, as in *Bucephalandra* (Bogner, 1980) and many Arinae. In a few species of *Theriophonum* and *Typhonium*, distinct morphs of sterile flowers occur in the upper and lower parts of the central sterile region; these are believed to represent sterile male and female flowers, respectively (Engler, 1920a).

For a more complete discussion of the morphology and spatial distribution of sterile flowers in araceous inflorescences, see Grayum (1984).

Compound inflorescences. Given that "first-order" inflorescences (i.e., spadices) in Araceae are often functionally analogous to single flowers, it is not surprising that they are frequently associated in "second-order," or compound, inflorescences.

Ray (1987b, 1988) analyzed and placed in tentative evolutionary and ecological perspective the various growth phenomena resulting in the production of compound inflorescences in Araceae.

Ray (1988) pointed out that, with the exception of *Orontium*, all Araceae with bisexual flowers have either no bud or merely a vegetative bud on the peduncle base and never develop multiple inflorescences (he dismissed the complex and unique "inflorescence sympodium" of *Gymnostachys* as a "condensed shoot system"). Based partly on this observation, he reasoned that the inability to produce paired or compound inflorescences is the primitive condition in Araceae; species able to develop but a single inflorescence per article were deemed relatively inflexible reproductively, such that selection would tend to favor "short, possibly homeophyllous articles" in order that "potential inflorescences" might be produced "as frequently as possible." But since this would tend to prevent seasonal flowering, such species "would need to mature all of these inflorescences" in order to maximize reproductive potential (Ray, 1988). *Anthurium* is cited as an exemplar of this continuous, aseasonal flowering strategy, necessitated by an inability to produce compound inflorescences.

Reproductive flexibility is increased somewhat by the ability to produce two inflorescences per article, considered the next most advanced state by Ray (1988). In *Orontium*, *Anubias*, *Peltandra*, *Alocasia*, *Caladium*, *Spathicarpa*, and *Callopsis* (among those genera studied by Ray), a second inflorescence is produced from a bud at the base of the original peduncle (Ray, 1988). Compound inflorescences in these genera are determinate, however: no further proliferation is possible, since the second peduncle lacks a bud.

Intermittent homeophyllous growth is seen as a means for aroid species with a fixed one or two inflorescences per article of overcoming this limitation and achieving a modicum of reproductive flexibility by allowing for "the relatively rapid serial production of inflorescences" within a specified season (Ray, 1988). It is, in fact, known only from species in this category. As defined in a previous section, intermittent homeophyllous growth involves an alternation of anisophyllous and homeophyllous phases. Various subtypes are recognized (Ray, 1987b), according to the number of leaves per homeophyllous article.

Intermittent diphyllous growth is the most familiar type, occurring in most species of *Monstera* and in *Anadendrum* (Ray, 1988). The diphyllous phase is associated with flowering and produces what is in effect a compound inflorescence. Although the spadices are solitary in the axils of the sympodial leaves, the compound effect is achieved by a condensation of the axis and by the fact that both leaves (the prophyll and sympodial leaf) of each diphyllous article are cataphylls. At the time of anthesis, the diphyllous "compound inflorescences" of these species generally terminate the shoots.

Intermittent triphyllous sympodial growth, so far observed only in *Rhodospatha* and *Alocasia*, interposes a mesophyll between the prophyll and sympodial cataphyll in the homeophyllous articles. In *Alocasia*, each article terminates in paired inflorescences, and the mesophylls are foliage leaves (Ray, 1988). Intermittent tetraphyllous growth is hypothetical (Ray, 1987b).

Monophyllous homeophyllous sympodial growth results in the production of indeterminate, condensed "inflorescence sympodia," each consisting of as many as 10 or more "first-order" inflorescences, in the axils of individual sympodial leaves on the shoot (Ray, 1988). Each "first-order" inflorescence is terminal on an article bearing a single leaf, the bracteole (always a cataphyll).

Three distinct types of monophyllous growth occur in Araceae. (1) Axillary growth, in which each succeeding inflorescence develops from a bud in the axil of the bracteole of the next lower order, is known only from *Dieffenbachia* and *Philodendron*, including species of subg. *Pteromischum*. (2) Gorgonoid growth, in which each succeeding inflorescence develops from a bud on the internode below and opposite to the bracteole, is known from *Aglaonema*, *Syngonium*, and *Xanthosoma*. (3) Mixed axillary gorgonoid growth is an alternation of the above two types and is known only from *Homalomena rubescens*. Presumably monophyllous inflorescence sympodia are known from many other genera than analyzed by Ray (see e.g., Grayum, 1984), and the application of his techniques to these is desirable.

Production of inflorescence sympodia by axillary, gorgonoid, or mixed monophyllous homeophyllous growth is considered the most advanced condition in Araceae. Species in this category are able to take maximum advantage of the best season for reproduction by producing a theoretically unlimited number of inflorescences from the axil of a single sympodial leaf (Ray, 1988).

Individual flowers: general considerations. All aroid flowers are actinomorphic and hypogynous, or fundamentally so. Various authors (Eyde et al., 1967; Hotta, 1971; Barabé, 1982) have described the ovary in *Lysichiton* and species of *Pothos* and

Cyrtosperma as "partly inferior," and Barabé et al. (1987) insisted that that of *Symplocarpus* is truly inferior. According to Engler (1884) and Krause (1908), by contrast, the flowers of these genera are deeply embedded in the axis of the inflorescence. Either condition must be regarded as derived (Eyde, 1975).

All bisexual aroid flowers that have been studied are protogynous (Engler, 1905; Engler & Krause, 1908; Krause, 1908; Engler, 1911), and most monoecious aroid inflorescences appear to exhibit second-order protogyny (see e.g., Gottsberger & Amaral, 1984). To date, the sole exception is *Arisarum simorrhinum*, in which stigma receptivity and anther dehiscence are said to coincide (Herrera, 1988). Protogyny is quite uncommon among flowering plants (Bawa & Beach, 1981) and is frequently seen in association with beetle pollination (Gottsberger, 1977; Bullock, 1981).

The perianth. Araceous flowers may be characterized either by the presence or absence of a perianth (or perigonium). The distribution of the two conditions is correlated with floral sexuality: Araceae that regularly have unisexual flowers lack a perianth, with the exception of *Stylochaeton* and the Zamioculcadeae. The reverse correlation is slightly weaker: *Calla*, *Pycnospatha*, *Heteropsis* and all Monstereae have naked, bisexual flowers.

There is little question that naked flowers have been derived from perigoniate ones in Araceae (Engler, 1884), as is the general trend in monocots (Howarth, 1957). Moreover, unisexual flowers and naked flowers have evolved repeatedly within the family (Grayum, 1984).

The aroid perianth is always reduced, wholly sepaloid, and rarely any color other than greenish or brownish, and probably plays little if any role in pollination. There are always two alternating whorls of tepals (Engler, 1884), the total number generally being either four or six. The presumed transition from trimery to dimery appears to be relatively simple and to have occurred independently on many occasions; several genera contain species in each category, and the condition may vary on individuals, even within the same spadix (Engler, 1884).

In *Anadendrum*, *Spathiphyllum* sect. *Massowia*, *Holochlamys*, and *Stylochaeton* the tepals are completely fused into a rotate to cupulate or urceolate perianth. This is certainly a derived condition (Howarth, 1957). The perianth is dimorphic in *Stylochaeton*, being rotate in the male and urceolate in the female flowers (Engler, 1920a). Hotta (1976) reported a connate perianth in *Pedicellarum*, but in the material I examined (*Martin & Ismawi S36660* MO) the six tepals are entirely distinct and in two whorls, just as in *Pothos*.

Araceous tepals generally have a single vascular trace, but in *Symplocarpus* and *Podolasia* these are branched. Tepals in *Zamioculcas* each have three traces (Hotta, 1971).

Valvate aestivation of the perianth is said to represent the primitive condition in Araceae (Engler, 1920b); however, in *Podolasia*, *Dracontium* (Engler, 1911), and all three genera of the tribe Orontieae (Krause, 1908) aestivation has been reported as imbricate. These may represent cases in which basically valvate aestivation has been distorted, as suggested by Engler (1920b), but the distribution of this character state among such phenetically primitive genera warrants further investigation.

The androecium. Stamen morphology varies greatly in Araceae. Most Araceae have rather short (later elongating), broad, flat filaments topped by smallish, basifixed anthers. The stamens of Potheae, *Anthurium*, and the Lasieae are especially similar in this respect (Engler, 1911). On the other hand, nearly all monoecious species have thick, short, often prismatic, flat-topped stamens, frequently with lateral anthers. Engler's (1884) explanation is that stamens deprived of the protection of a perianth need to be sturdier.

Long, slender filaments are uncommon in Araceae, occurring, for example, in *Pseudodracontium*, *Stylochaeton*, *Arisarum*, and in the synandria of *Arisaema* and most Spathicarpeae (Engler, 1920a).

The stamens of perigoniate aroid flowers are generally the same number as the tepals and opposite them, in two whorls (Eyde et al., 1967; Cronquist, 1981). Thus, rarely are there more than six stamens per flower. In some species of *Dracontium*, however, there may be a third whorl, for a total of 9–12 stamens (Engler, 1911, 1920b).

The stamens of all naked, unisexual flowers are considered to be reduced to a single whorl (Engler, 1884). The number of stamens per flower is thus usually reduced, frequently to three or two and, in a few cases, to just one (*Colletogyne*, *Filarum*, some species of *Biarum*, *Arisarum*, and other genera). At the other extreme, the synandria of male flowers of *Typhonodorum* may comprise up to eight stamens, those of some species of *Alocasia* as many as 12.

Stamens may be so crowded and irregularly arranged on the spadix in some monoecious aroids that it is difficult or sometimes impossible to be sure how many compose a single flower; this is the

case, for example, in *Ambrosina* (Engler, 1920a) and the subtribe Arinae (van Tieghem, 1907). The stamens in the *Philodendron* type of male flower, on the other hand, are more or less polygonal and fit together like pie slices in each male flower, so that the number of stamens per flower is obvious. This type of stamen occurs also in *Culcasia*, *Pseudohydrosme*, Nephthytideae, *Montrichardia*, and *Homalomena*. The number of stamens per flower in these groups may vary greatly on the same spadix, as Engler (1884) has documented for *Homalomena rubescens*.

French (1986b) surveyed stamen vasculature in Araceae and reported that virtually all genera with bisexual flowers have 1–3 unbranched bundles per stamen, certainly the primitive condition for the family. Stamens of the remaining genera have either forked or anastomosing bundles.

Barabé & Labrecque (1983) suggested that some of the stamens in the naked flowers of *Calla* may be tepalar in origin.

The anthers of Araceae are basically tetrasporangiate and dithecal, as for angiosperms in general; cases of reduction in the number of sporangia are few (see Grayum, in press b). In *Synandrospadix*, the upper male flowers have disporangiate anthers, while the anthers of the central bisexual flowers are tetrasporangiate (Cocucci, 1966). The anthers of all Araceae are supposed to be impeltate (basifixed) (Dahlgren & Clifford, 1982).

The mode of anther dehiscence in Araceae is somewhat correlated with sexuality. Dehiscence by longitudinal slits appears to be the primitive condition and is common only in taxa with bisexual flowers (i.e., Pothoideae, Monsteroideae, Calloideae, and Lasieae). Only a few monoecious genera have fully longitudinal anther dehiscence (see Table 3). The tendency is for these slits to become confined to the apical half of the anther, as in *Heteropsis* and *Cyrtosperma*, and ultimately to be reduced to apical pores, as in most monoecious genera, in which the male flowers tend to be densely packed. In some species of *Lagenandra* and *Cryptocoryne*, the pore is located at the apex of a conical tube. In *Bucephalandra*, *Aridarum*, and *Phymatarum*, each anther sac is surmounted by a horn; the pollen exits through a pore formed by the abscission of the apical part of the horn (Hotta, 1971).

In a few taxa, such as *Zomicarpa* and some species of *Homalomena* and *Arisaema*, the anthers dehisce by an apical transverse slit.

Anther dehiscence in Araceae is virtually always extrorse. Although Hotta (1976) reported introrse dehiscence in *Pedicellarum*, my examination of the specimen *Martin & Ismawi S36660* (MO) showed anther dehiscence to be unequivocally extrorse. However, Engler (1905) reported introrse dehiscence in *Zamioculcas*, and Bogner (in litt.) has recently confirmed this.

In many monoecious Araceae the stamens are connate in the male flowers, forming synandria (this detail was overlooked by Dahlgren & Clifford, 1982). In most cases the fusion involves only the filaments; however, in a few species of *Arisaema* the anthers also are partially or fully (Sivadasan & Sathish Kumar, 1987) connate. Synandria are most characteristic of Colocasioideae, where they occur exclusively in every genus. They are fairly frequent in Engler's Philodendroideae and Aroideae, and also occur in *Gonatopus* and *Pistia*.

In the simplest synandria the filaments are fused only toward the base. This condition occurs in some Schismatoglottidinae, *Carlephyton*, *Gorgonidium*, *Dracunculus*, and many species of *Arisaema*. The most specialized type is found throughout the Colocasioideae, in which the filaments, though completely united, are basically short and thick with the anthers borne laterally or at the upper margin of the more or less flat-topped, polygonal structure. This type of synandrium also occurs in *Anubias*, *Bognera*, *Dieffenbachia*, *Typhonodorum*, *Peltandra*, *Arophyton*, and *Protarum*. These synandria much resemble, and are no doubt derived from, the *Philodendron* type of male flower, discussed previously; in some species sutures may still be observed where the individual stamens must have fused.

Rarely synandria belonging to adjacent male flowers may fuse. In the apical part of the spadix of *Gorgonidium mirabile*, for example, numerous stamens may become united into branched, dendritic "super-synandria" in which the limits of individual flowers are impossible to define. The situation in *Ariopsis* is even more remarkable: adjacent synandria are connate laterally into a massive superstructure involving the entire male portion of the spadix, analogous to the syncarps of genera such as *Syngonium* and *Cryptocoryne*.

Staminodia are usually the sole components of sterile male flowers in Araceae. In genera with distinct fertile stamens the sterile male flowers (if present) generally have distinct staminodia. Likewise, where fertile stamens are connate into synandria, staminodia (where present) are connate into synandrodia. *Dieffenbachia*, with connate fertile stamens but sterile flowers with distinct staminodia, is the sole exception to this rule (Engler, 1884).

Staminodia associated with female flowers are encountered in *Amorphophallus* subg. *Metan-*

drium (Stapf, 1923), several genera of Philodendroideae, and a few Aroideae. In Colocasioideae only *Steudnera* has staminodia in the female flowers. Contrary to the rule for sterile male flowers, staminodia in female flowers are generally distinct, even in genera with connate fertile stamens. This suggests that monoecy evolved prior to stamen connation in these groups. Female flowers with synandrodia are known only in *Peltandra*, *Astero-stigma* sect. *Rhopalostigma*, and all Arophyteae (Bogner, 1972).

The number of staminodia associated with each female flower, in cases where these staminodia are distinct, probably corresponds primitively to the number of stamens per fertile male flower. This correspondence is a frequent condition in Araceae. However, female flowers of *Typhonodorum*, *Steudnera*, and *Spathicarpa* typically have fewer staminodia than fertile stamens, and the number is typically reduced to just one in *Homalomena* (Engler, 1884), and occasionally in *Schismatoglottis*, *Hottarum*, and *Aglaonema* as well. On the other hand, there are more staminodia in female flowers of *Protarum* than fertile stamens in the male flowers (Engler, 1920b).

The function of staminodia in female flowers is not usually known; Engler (1884) ascribed a protective function to the tepaloid staminodia of *Zantedeschia aethiopica* as well as to the perianthlike synandrodia of *Peltandra*. Staminodia of *Spathicarpa* (Troll, 1928) and of *Aglaonema* (Daumann, 1930) appear to secrete nectar.

Additional aspects of androecium morphology in the Araceae are discussed in Grayum (in press b).

The gynoecium. The gynoecium in all known Araceae is unipistillate. The style is generally short and thick to conical; often it is entirely absent, and the frequently discoid stigma is thus sessile on the ovary. Long narrow styles are rare (as in species of *Anthurium*, *Symplocarpus*, *Dracontium*, *Pycnospatha*, some species of *Amorphophallus* and *Philodendron*, *Stylochaeton*, some Spathicarpeae, and *Ambrosina*), and the stigma is never elongate. According to Engler (1920a), most aroids have a densely papillate stigma, although Heslop-Harrison & Shivanna (1977) described the stigma of *Alocasia* as smooth. Mayo's (1989) detailed studies of style and stigma characters in *Philodendron* suggest that these organs deserve more intensive study throughout the family.

In perigoniate or bisexual flowers, the number of locules in the ovary is generally equal to half the number of tepals (or stamens), so that species with six tepals per flower have fundamentally three-loculed ovaries, and species with four tepals fundamentally two-loculed ovaries. Reduction to a single locule is frequent, however, throughout Araceae. A few taxa may have an unusually high number of locules, for example, *Spathantheum* (6–8) and *Philodendron* (to 12–14 in a few species, to as many as 47 in subg. *Meconostigma*; Mayo, 1989).

Placentation is correlated with loculization to a certain extent. All Araceae with more than one locule in the ovary have some type of axile placentation (a circumstance overlooked by Dahlgren & Clifford, 1982). Three variations of axile placentation are known in Araceae: ovules may be borne along the entire length of the placentae (the rarest condition), or they may be reduced to one or a few borne either at the base or in the middle (both comparatively common; see Table 3).

Aroid genera with unilocular ovaries may have parietal, basal, apical, or both basal and apical placentation. The first two conditions are most common. In parietal placentation, the number of placentae varies from one (e.g., *Arum*) to many (e.g., *Homalomena*). Apical placentation is known only from *Gymnostachys*, *Symplocarpus*, and *Lasia*; apical and basal placentation in the same ovary occurs in *Dracunculus*, *Helicodiceros*, *Theriophonum*, and *Heteroaridarum*, although in the last-mentioned genus the apical placenta is sterile (Hotta, 1976).

Apical and basal placentation types have in some cases clearly been derived from parietal placentation, with the development of just one or a few ovules at a particular locus on the placenta. For example, in some species of *Epipremnum* with basal placentation, the largely naked placenta extends the entire length of the ovary. Other species in the same genus have typical parietal placentation. Hotta (1971), based on a study of ovary vascularization, concluded that basal placentation was derived from parietal in *Alocasia* as well. That basal placentation may also be directly derived from axile placentation, on the other hand, is suggested by the situation in *Culcasia*, where some species have two- or three-loculed ovaries with axile placentation (basal subtype), while others have unilocular ovaries with basal placentation. Furthermore, in *Holochlamys* (with unilocular, multiovulate ovaries) there is evidence of a basal vascularized septum, indicating derivation from a plurilocular ovary with axile placentation, such as occurs in the closely related genus *Spathiphyllum* (Eyde et al., 1967). A similar situation seems to occur in *Calla* (Barabé & Labrecque, 1983).

Spathicarpa, with unilocular, uniovulate ova-

ries and basal placentation, possesses an apical pendent lobe within the ovarian cavity that is interpreted as the vestige of a septum (Engler, 1884; see also Barabé & Chrétien, 1985). The closest relatives of *Spathicarpa* are all plurilocular with axile placentation.

Thus it seems clear that basal (and presumably apical) placentation in Araceae may be derived directly from either axile or parietal placentation but must in either case be considered an advanced condition. Parietal placentation is here considered to have been derived in all cases from axile placentation via the intrusive-parietal intermediate stage, which is widespread in Araceae (see Table 3). This conclusion follows inevitably if derivation of unilocular ovaries from plurilocular ovaries is accepted as universal. This view receives support from Puri (1952), who concluded that parietal placentation is always derived from axile placentation in angiosperms as a whole. Since the derivation of basal and apical placentation from the parietal or axile conditions necessarily involves a reduction in ovule number, it also follows that multiovulate placentae are generally more primitive than few-ovuled placentae, as Engler (1884) concluded. This is a very strong trend in monocots in general according to Howarth (1957), and Eyde (1975) stated that the reverse trend is known in no group of angiosperms.

The pluricarpellate nature of unilocular ovaries in Araceae is generally easily established on the basis of such criteria as number of placentae (in species with parietal placentation), number of stigma lobes, multiples of ovules, and ovarian vasculature (see, e.g., Krause, 1908; Eyde et al., 1967; Hotta, 1971; Barabé, 1982; Barabé & Chrétien, 1985; Barabé & Labrecque, 1983, 1984, 1985; specific examples are discussed in Grayum, 1984). In other cases (e.g., *Cyrtosperma*, *Lasia*, *Aglaodorum*, and *Spathicarpa*), putatively pseudomonomerous ovaries can be homologized with indubitably pluricarpellate ovaries of related genera (Engler, 1884). The diagnosis of pseudomonomery in these cases may be bolstered by occasional observations of excentric sterile locules, sterile placentae (see Eyde et al., 1967), vestigial septa, extra vascular bundles, or variation in the orientation of placentae in flowers of the same spadix (Engler, 1884; Eckardt, 1937).

Most Araceae, then, are either plainly syncarpous or else have pseudomonomerous ovaries that can be homologized with clearly syncarpous ovaries of related genera. *Pistia* and most of Engler's Aroideae, however, have unilocular ovaries with basal and/or apical placentation or with a single parietal (marginal?) placenta, and have no close relatives generally acknowledged to be syncarpous. Engler (1884) categorized these unilocular genera as unicarpellate and apparently believed them to be primitively so; Dahlgren & Clifford (1982) adopted the same view. By contrast, I believe these to represent products of reduction from syncarpy, for the following reasons. (1) The flowers and inflorescences of these genera are in all other respects among the most advanced of any Araceae. (2) The Aroideae and *Pistia* are in my estimation (this will be discussed later) rather closely related to the basically syncarpous Thomsonieae. (3) In such a large family containing both syncarpous and unicarpellate gynoecia, surely we ought to find a few species with pluripistillate, apocarpous gynoecia, but there is not even the slightest hint of such a condition within the family. (4) Arber (1925) and Eckardt (1937) reported the occasional presence of a second placenta in *Arum*.

The hypothetical aroid ancestor must have had syncarpous, plurilocular ovaries with multiovulate, axile placentation. There is no strong evidence for apocarpy, unipistillate or pluripistillate, anywhere within the family. Pervasive throughout the Araceae are trends toward pseudomonomerous, unilocular ovaries with pauciovulate, parietal to basal and/or apical placentation. But it is likely that high ovule number and high locule number have occasionally been secondarily derived. *Furtadoa*, in which the number of ovules in the unilocular ovaries varies from 15 to 20 in the lowermost flowers to five, three, or even one in the uppermost female flowers of the same spadix (Hotta, 1981), may best exemplify a secondary increase in ovule number (see Grayum, 1984, for additional candidates). The high locule numbers noted previously for some species of *Philodendron* probably reflect a secondary increase in carpel number, as Engler (1884) originally hypothesized, in spite of the assertion of Eyde et al. (1967) that "it would strain credulity" to postulate any such increase. Evidence for this secondary increase is provided in Grayum (1984). Mayo (1986) proposed that high locule numbers in *Philodendron* may have evolved in response to gall wasp parasitism.

The primitive carpel number of Araceae is certainly either two or three, though there appears to be little basis within the family for selecting between these alternatives. The conversion from dimery to trimery or vice versa seems rather trivial and to have occurred independently any number of times, at least among hermaphroditic taxa. Both floral

plans are frequent and occur together in several genera (*Rhaphidophora, Rhodospatha, Spathiphyllum, Orontium, Cyrtosperma, Lasia, Podolasia, Urospatha,* and *Dracontium*), often in the same species or even on the same spadix. The same tendency can also be seen in the ovaries of some monoecious genera (see Grayum, 1984, for a list). Several clues, however, suggest that trimery is perhaps more primitive (see Grayum, 1984), and this is by far the most common condition in monocots as a whole, although the same duality occurring in Araceae is widespread in putatively related monocot families (Burger, 1977).

As with male flowers, adjacent female flowers in Araceae may become fused to one another on the spadix. This is obviously a derived condition. The tendency is most pronounced in New World Colocasioideae. Pistils of *Xanthosoma* and *Aphyllarum* have thick, spreading, discoid styles that are coherent with those of adjacent pistils (Madison, 1981). In *Syngonium*, the ovaries themselves are connate, resulting in a syncarpous multiple fruiting body. This also occurs in *Cryptocoryne* and *Piptospatha* sect. *Gamogyne*.

The stylar regions of adjacent bisexual flowers in most Monstereae become fused following abscission of the stamens, thus forming a mantle that is shed as a unit, exposing the seeds upon ripening (Engler & Krause, 1908).

Pistillodes in association with fertile male flowers are less common than the converse situation. Not surprisingly, pistillodes are seen to best advantage in those few genera with perigoniate, unisexual flowers: *Zamioculcas, Gonatopus,* and *Stylochaeton*. These are usually much-reduced structures, but in *Zamioculcas* sterile ovules are still evident in the pistillodes of male flowers (Engler, 1884).

In genera with naked flowers, evidence (if any) of a vestigial gynoecium is usually limited to a central, vacant spot, as in the lower male flowers of some species of *Amorphophallus, Dieffenbachia,* and *Taccarum,* or to the presence of a central, free-standing vascular trace, as in the synandria of some *Colocasia* and *Arisaema* species (Hotta, 1971). Actual pistillodes occur with regularity only in *Furtadoa,* where a conspicuous pistillode accompanies each male flower nearly to the tip of the spadix (Hotta, 1981). No function is yet known for these.

Ovule morphology and orientation in Araceae are fully discussed in Grayum (in press b); see Table 4 for polarities of important characters. French (1986c) reinvestigated aroid ovule orientation, and his results are included in Table 3. One of French's more significant findings is that the traditional system of classification of ovule orientation types, i.e., as "orthotropous," "anatropous," etc., is apparently inadequate in Araceae; for example, orthotropous ovules in Philodendroideae and Colocasioideae differ significantly from those of Aroideae and are probably not homologous for this condition.

French (1986c) also systematically surveyed ovary vasculature, characterizing three main patterns (simple bundles, multiple dorsal chalazal bundles, and radially symmetric chalazal bundles) highly correlated with ovule orientation and, somewhat more weakly, with ovule number and size. Simple bundles are the most widespread condition, and are exclusive to Araceae with bisexual flowers and/or a perianth; they are probably primitive.

Fruits and seeds of Araceae have yet to be studied adequately, since these structures often fail to develop in greenhouse situations (Engler, 1884). As far as is known, aroid fruits are always berries. Since fleshy fruits are generally believed to have been derived from dehiscent fruits (Roth, 1977), this feature can be regarded as one of the few synapomorphies for the family Araceae. Araceous berries may be one- to many-seeded, but there is never a bony endocarp. Dahlgren & Clifford's (1982) report of drupes in *Pistia* is in error (see, e.g., Crisci, 1971; Mercado-Noriel & Mercado, 1978; da Silva, 1981). The berries of *Lagenandra* are said to dehisce basally, releasing the seeds (Bogner, 1987); however, in most cases aroid fruits are probably bird (Peckover, 1985; Shaw et al., 1985) or bat (Bogner, 1987) dispersed. Seed morphology and endosperm retention in Araceae are discussed in detail in Grayum (in press b; see also Tables 3 and 4 in the present paper).

Nectaries. Septal (gynoecial) nectaries, recorded from many monocot families including palms, do not occur in Araceae. Dahlgren & Clifford (1982) recorded only stigmatic secretions and an occasional instance of perigonal nectaries (e.g., *Anthurium*) from Araceae. However, staminodial nectaries occur in *Spathicarpa* (Troll, 1928), and probably also in *Aglaonema* (Daumann, 1930); sterile bisexual flowers may function similarly in *Monstera* (Madison, 1977; Ramírez & Gómez, 1978; Ramírez, 1980, 1987).

Extrafloral nectaries have only rarely been reported for Araceae, for example, at the apex of the petiole in *Philodendron myrmecophilum* (Madison, 1979b). J. C. French (pers. comm.) has found anatomically defined extrafloral nectaries only

TABLE 4. Summary of taxonomically useful characters in the Araceae.

Characters	Primitive conditions	Advanced conditions
Growth habit	rhizomatous or caulescent	tuberous, epiphytic, vining
Phyllotaxy	distichous	spiral
Geniculum	absent	present
Leaf form	simple, cordate	lanceolate; compound or lobed
Leaf venation	parallel	reticulate
Stomata	paracytic?	anomocytic, tetracytic
Compound vascular bundles	absent	present
Cortical vascular system	absent	present
Stem endodermis	absent	present
Trichosclereids	absent	present
Secretion vessels	absent or single cells	"laticifers"
Biforines	absent	present
Prisms	absent	present
Spathe	Type I	Types II, III, & IV
Spadix	hermaphroditic	monoecious
Perigonium	present	absent or fused
Locules of ovary	2 or 3	one or many
Ovules per locule	many	few or one
Placentation	axile	parietal, basal, apical
Stamen length	elongate	stout
Number of stamens	4–6	fewer or more
Anther dehiscence	longitudinal	apical, lateral, poricidal
Staminodia in female flowers	present	absent or fused
Ovule type	anatropous	orthotropous
Nucellus type	crassinucellate	tenuinucellate
Megaspore units	tetrads	dyads
Endosperm in seed	present	absent
Cells of chalazal chamber	6–8	1–4
Base chromosome number	$x = 7$ or 14	$x = 15, 16, 17, 18, 19, 20$, etc.
Pollen aperture type	monosulcate	zonate, forate, inaperturate
Pollen shape	boat-shaped	globose
Pollen size	medium-sized	small, large, very large
Pollen-unit	monads	tetrads
Exine sculpturing	foveolate-reticulate	striate, psilate, spinose, etc.
Pollen starch content	absent	present
Pollen nuclear number	II	III

in Engler's subfamilies Lasioideae (8 of 11 genera examined) and Philodendroideae (*Philodendron*, *Homalomena*, *Aglaonema*, and *Anubias*).

EMBRYOLOGY

Systematically important aspects of aroid embryology have been recently and exhaustively reviewed elsewhere (Grayum, 1985, 1986a, in press b; also see Tables 3 and 4).

Based on the available evidence, the Araceae appear quite as variable embryologically as in most other regards. Intrafamilial variation in many characters, such as nucellar development, embryogeny, and endosperm development, is intriguing and probably of great systematic importance. However, with the exception of a few comparatively unimportant characters (anther endothecium type, pollen nuclear number, pollen starch content, ovule orientation, and endosperm retention), information in most embryological subfields is available for only a handful of aroid genera.

Embryological character states that appear invariable in Araceae include extrorse anther dehiscence, periplasmodial anther tapetum with uninucleate cells, absence of perisperm, and helobial (haustorial) endosperm development. All other important characters vary, but the hypothetical aroid ancestor is considered to have had four microsporangia per anther; endothecial thickenings present; isobilateral microspore tetrads; binucleate, starchless pollen at anthesis; bitegmic, anatropous, crassinucellate ovules with a thick nucellar cap; uni-

cellular ovule archesporia; megaspores in tetrads, with the chalazal one functional; *Polygonum*-type embryo sacs; solanad or caryophyllad embryogeny; *ab initio* cellular division in the micropylar endosperm chamber; 2–8 cells in the chalazal endosperm chamber; and endosperm retained in the ripe seeds. Some important apomorphic variations on these themes are discussed under the individual taxonomic headings in the second half of this paper.

POLLEN MORPHOLOGY

Pollen morphology of Araceae has recently been reviewed in detail by Grayum (in press a). Reference should be made to that paper, which includes scanning electron micrographs of pollen for most genera, and to Table 4 in the present paper; the definitive light-microscopy survey of aroid pollen is by Thanikaimoni (1969).

External pollen morphology is exceptionally variable within the Araceae. Internal exine structure is probably equally variable, although as yet little studied. The most primitive araceous pollen is regarded as monosulcate, boat-shaped, heteropolar, bilaterally symmetrical, and small to medium-sized (22–34 μm in maximum diameter). It is shed in monads, has foveolate to reticulate exine sculpturing, and is probably tectate-columellate (Grayum, in press a). The most advanced pollen is held to be inaperturate, globose, apolar, and radiosymmetric. Exine sculpturing is exceedingly variable; the evolutionary derivation of the various forms is complex, with similar types having evidently been derived via two or more different pathways (see Grayum, in press a). This is the case with psilate and spinose exines, considered the most highly derived conditions; these two types are closely correlated with, and presumably specialized for, beetle and fly pollination modes, respectively (Grayum, 1986b).

POLLINATION BIOLOGY

Data on pollination biology for the majority of Araceae are still very meager. This is especially true in the case of tropical species, which compose the bulk of the family. Pollination in the vast genus *Philodendron*, for example, is mainly known only from a few studies on two species of subg. *Meconostigma* (see, e.g., Gottsberger & Amaral, 1984), and no careful field study of pollination in *Anthurium* has been published. The only tropical aroid genus that is somewhat well known in this regard is *Amorphophallus*, mainly from the work of van der Pijl (1937, 1953). Phylogenetically critical taxa (such as Potheae and Lasieae) with primitive floral and pollen characters are in particular need of study. Even the temperate aroids, with the exception of the mainly European genera *Arum* and *Dracunculus*, are surprisingly poorly known in terms of pollination biology.

Data on aroid pollinators were summarized by Grayum (1984, 1986b), including only field studies conducted in natural habitats. Even with this restriction, the data must be evaluated carefully, since many are superficial or anecdotal. The broadest generalization that can be made is that Araceae are, as far as is known, exclusively entomophilous. The overwhelming majority of species are pollinated by beetles and/or flies. North American species of *Arisaema* have variously been said to be pollinated by thrips (Rust, 1980), by flies (Bierzychudek, 1982), or by both (Rock, 1952).

Bee pollination occurs rarely in Araceae. It is confirmed only in species of *Anthurium* and *Spathiphyllum* (Williams & Dressler, 1976), reported in *Dracunculus canariensis* (Boyce, 1986), and suspected in some *Syngonium* species (Madison, 1979a; pers. obs.). Madison (1979a) described *Montrichardia* as pollinated by "bees, presumably"; however, dynastine scarab beetles have recently been collected from spathes of *M. arborescens* in Costa Rica (M. Grayum & G. Schatz, unpublished data). Species of *Monstera* have also been reported as bee-pollinated (Madison, 1977; Ramírez & Gómez, 1978), but these reports are also dubious; at least two species of the closely related and florally similar genus *Rhodospatha* are now definitely known to be beetle-pollinated (G. Schatz & M. Grayum, unpublished data), and dynastine scarab beetles were recently discovered in inflorescences of *Monstera oreophila* in Chiriquí, Panama (M. Grayum, unpublished data). *Symplocarpus foetidus* has been said to be partly pollinated by hive bees (Trelease, 1879) in North America, where *Apis mellifera* is not native.

Beetle pollination in neotropical aroids virtually always involves large scarab beetles of subfamily Dynastinae of the family Scarabaeidae. Pollination by dynastine scarabs is now documented or strongly indicated for species of *Monstera*, *Rhodospatha*, *Homalomena*, *Philodendron*, *Dieffenbachia* (Young, 1986), *Montrichardia*, *Caladium*, *Xanthosoma*, and *Syngonium* and is perhaps general throughout most of these genera. Dynastine scarabs have even been collected from spathes of a *Homalomena* species in Malaya (G. Schatz, pers. comm.). Beetle-pollinated paleotropical aroids more commonly attract beetles of other taxa, mainly Nitidulidae (see, e.g., Thompson & Rawlins, 1986), though other groups (nondynastine Scarabaeidae,

Scaphidiidae, Staphylinidae, Dermestidae, Scydmaenidae, Silphidae) are occasionally implicated. The north temperate *Lysichiton americanus* is pollinated by staphylinids (Pellmyr & Patt, 1986). These beetles appear to have a less specialized relationship with Araceae than do the dynastine scarabs; several families are frequently reported together on a single inflorescence, often along with one or more families of flies (see, e.g., Bogner, 1976a, 1981a; Dakwale & Bhatnagar, 1985).

Fly-pollinated aroids are mainly temperate or paleotropical; a few neotropical taxa, most notably species of *Dracontium*, are strongly suspected to be myiophilous. The flies involved are usually small, weak-flying types, such as fungus-gnats, fruit-flies, and various blood-sucking midges. Apparently they are deceived into entering aroid spathes by olfactory and perhaps other cues. Most frequently mentioned are the families Mycetophilidae and Drosophilidae; others include Syrphidae, Chloropidae, Muscidae, Anthomyiidae, Centropogonidae, Simuliidae, Psychodidae, Sphaeroceridae, Calliphoridae, Sciaridae, and Culicidae.

Fly and beetle pollination in Araceae are usually attended by complex and obviously highly evolved morphological, behavioral, and physiological specializations on the part of the plant species, including enclosing, constricting spathes (sometimes secreting resin); unisexual, naked flowers segregated on the spadix; and often highly modified sterile flowers in one or more positions on the spadix, presumed or known to function, e.g., as food rewards for pollinators, or in nectar secretion, occlusion of the spathe orifice or (at least in the case of naked, terminal appendages) in the production of heat and/or odors.

Pollen exine sculpturing is strongly correlated with pollination mode in Araceae. This notion apparently first surfaced in the literature as the following observation by Rock (1952: 73) concerning the North American species *Arisaema atrorubens* (= *A. triphyllum*): "The pollen grains appear to be especially designed for dispersal by insects; the tiny spherical grains are covered with numerous barbed spines." Strong, family-wide correlations of spinose pollen with fly pollination and psilate pollen with beetle pollination have recently been documented (Grayum, 1986b), even if functional relationships such as that implied in Rock's statement have yet to be elucidated.

Thus beetle and fly pollination, which are basic to Araceae and associated with across-the-board specializations, are here regarded as primitive for Araceae. It is unclear which of these two modes might have characterized the hypothetical aroid ancestor. Out-group comparison suggests beetle pollination, which is much more common than fly pollination in palms, and is speculated to be more primitive in that family (Henderson, 1986). Cyclanthaceae, so far as is known, are also basically beetle-pollinated (see Beach, 1982). Pollination by families of smaller beetles, particularly Nitidulidae, is much more common among flowering plants in general than pollination by Scarabaeidae (see Grayum, 1984) and is perhaps more primitive within Araceae, even though it appears to be attended by less extensive specializations. Pollination by Nitidulidae and Curculionidae is especially widespread in palms (Henderson, 1986).

Bee pollination in Araceae is known with certainty only from genera with comparatively unspecialized floral and pollen morphology and is here considered a rather recent development within the family.

Some evidence suggests that the very earliest aroids or an immediate ancestor might have been wind-pollinated. The pollenkitt of Araceae, for example, is not typical of entomophilous angiosperms. Whereas entomophily normally implies sticky pollen, araceous pollenkitt is nearly always deficient, resulting, as for example in *Arum*, in dry pollen "equivalent to that of anemophilous angiosperms" (Hesse, 1980, 1981). Pohl (1931) reported that the pollenkitt of *Philodendron bipinnatifidum* is not resinous or oily as in most other angiosperms, but "plasma-like" and rapidly drying when exposed to air; it does not suffice to stick the pollen onto hard-bodied insects (this is apparently accomplished in *Philodendron* by means of a resinlike secretion of the inner surface of the spathe; see von Martius, 1831; Warming, 1883; Schrottky, 1910; Pohl, 1931; Gottsberger & Amaral, 1984; Mayo, 1986). Camazine & Niklas (1984) showed that *Symplocarpus foetidus*, a phenetically primitive species, has "a facultative capacity" for wind pollination. The possibility that Araceae may be derived from anemophilous ancestors certainly deserves further consideration.

Heat production in the vicinity of the inflorescence during anthesis is known from a wide range of aroids, including hermaphroditic genera, such as *Monstera* and *Symplocarpus* (Knutson, 1974) as well as monoecious genera in all major subfamilies. The exact site of heat production is the spadix, the energy being derived from respiration of starch (Knutson, 1974) or lipid (Seymour et al., 1984) contained in the rhizome or elsewhere.

The physiological literature on heat production by aroid inflorescences is voluminous but mostly divorced from taxonomic, evolutionary, and eco-

logical considerations. The exact function of heat production has been much debated; apparently there is a major role in attracting pollinators, but whether this is effected by the heat directly, or indirectly via an increase in the volatility of amines, indoles, etc., is a bone of contention (see, e.g., Moodie, 1976). The only paper of systematic significance is apparently that of Leick (1915), who recognized four main types of heat production among those Araceae for which this feature was then known, based on the periodicity of heating episodes and their localization on the spadix. As modified and augmented by Engler (1920b), these are: (1) the *Monstera* type, with three episodes on successive days, the middle one being strongest, and no marked localization; (2) the *Philodendron* type, with episodes on two successive days, the second stronger, localized in the male portion of the spadix; (3) the *Alocasia* type, with 3–5 maxima, the second being the main one, localized in the sterile apical appendage of the spadix; and (4) the *Arum* type (also known from *Sauromatum*, *Dracunculus*, and the Thomsonieae), with episodes on two successive days, the first being stronger and localized in the sterile appendage, the second (insignificant) episode confined to the male portion of the spadix.

Meeuse (1978) has offered a limited evolutionary interpretation of the various types of heat production in Araceae, suggesting that aroids with a more primitive inflorescence morphology, such as an open spathe, bisexual flowers, and other features, must have at least two heating episodes: one to attract pollinators, another to attract pollen vectors. More advanced aroids (with an enclosing or constricting spathe) can get away with a single pronounced heating episode at the time of stigma receptivity, since in effect they have a "captive audience" on hand for anther dehiscence. That such species yet retain weak, secondary heating episodes is taken as evidence that this type of heat production evolved from one of the more primitive types in Araceae rather than directly from an ancestor not exhibiting heat production.

KARYOLOGY

Data on aroid chromosome numbers available up to 1984 are assembled, tabulated, and discussed at length in Grayum (1984). The raw data will not be reproduced here but are frequently alluded to under the individual taxon headings in the second half of the present paper. Karyological data for the entire family Araceae are collated, revised, augmented, and analyzed in an important recent contribution by Petersen (1989), to which the reader is referred.

Among the polytypic aroid genera, only *Cryptocoryne* (Arends et al., 1982; Reumer, 1984), *Arisaema* (Hotta, 1971), *Amorphophallus* (Chauhan & Brandham, 1985), *Alocasia* (Bhattacharya,1974), *Arum* (Bedalov, 1981), *Biarum* (Talavera, 1976), and *Anthurium* (Sheffer & Croat, 1983) are reasonably well known chromosomally. The following relevant data can be distilled from the available counts in these and other genera. The lowest diploid number reported to be characteristic of any species in Araceae is $2n = 14$, occurring only in *Typhonium flagelliforme* (Ayyangar, 1973; $2n = 14$ has also been reported once for *Pistia stratiotes*, but $2n = 28$ is more typical of that species); the highest is $2n = 140$, in *Arisaema heterophyllum*. One of the most frequently reported diploid numbers in Araceae is $2n = 28$, and multiples of seven clearly prevail in the family. These considerations have led virtually all modern workers (Mookerjea, 1955; Larsen, 1969; Marchant, 1974; Raven, 1975; Ramachandran, 1978) to the conclusion that the primitive base number for the family is $x = 7$, which may also be the primitive base number for angiosperms as a whole (Raven, 1975). This is clearly the most reasonable viewpoint, considering the limitations of the data set, and is adopted here. It should be mentioned, however, that multiples of six appear to be disproportionately represented as base or co-base numbers among phenetically primitive aroids (see Grayum, 1984), e.g., those groups with bisexual flowers (most Pothoideae, Monsteroideae, Calloideae, and Lasieae). The putative sister-family Acoraceae is based on $x = 12$. Thus it may prove ultimately that Araceae are based on $x = 6$, even though multiples of six are now uncommon within the family.

A fair number of aroid genera appear to have base chromosome numbers that are not multiples of seven. Particularly common are $x = 16$, 17, 18, 19, and 20. Genera in this category largely comprise the subfamily Philodendroideae, as interpreted in this paper.

Although neither intrageneric polyploidy nor aneuploidy are pronounced features of Araceae (see Goldblatt, 1980; Arends et al., 1982; Sheffer & Croat, 1983), paleopolyploidy and aneuploidy have apparently played sizeable roles in chromosome evolution (Jones, 1957; Goldblatt, 1980; Sheffer & Croat, 1983). Even allowing for primary base numbers as high as $x = 13$, 82% of all araceous species counted are polyploids (i.e., $2n = 28$ or higher), as opposed to only 55% for monocots as a whole (Goldblatt, 1980).

The basic scenario for chromosome evolution in

Araceae (Jones, 1957; Larsen, 1969; Marchant, 1974) envisions the evolution of a (paleo)aneuploid series based on $x = 7$, giving rise to the primary base numbers $x = 6$, 8, 9, and perhaps even 5, 10, and 11. Subsequent doubling of chromosomes must then have resulted in euploid series based on these numbers, this in view of the fact that (aside from a very few counts of $2n = 14$, 16, 18, 20, and 22) no potential "paleodiploids" are known to exist. With a few minor reservations (see Grayum, 1984), this scheme is accepted here.

Another important process in aroid chromosome evolution may have been amphiploidy, which might explain the rather frequent occurrences of $2n = 26$, 30, and 34 on the basis of primordial hybridizations involving the primary base numbers 6 and 7, 7 and 8, and 8 and 9, respectively, to yield the secondary base numbers 13, 15, and 17 (Jones, 1957; Ramachandran, 1978). Amphiploidy may also explain some of the more unusual counts in Araceae, such as $2n = 22$ (a putative allotetraploid of 5 and 6, known only in the taxonomically disparate genera *Jasarum*, *Zomicarpa*, and *Ambrosina*) and $2n = 38$ (a putative allotetraploid of 9 and 10, occurring only in *Arophyton*, whose closest relatives have chromosomes in multiples of nine). Hybridization of extant aroid species in the field has rarely been reported, though it occurs, for example, in *Dieffenbachia* (H. J. Young, pers. comm.).

Of course, any of these putative amphiploids may equally well have arisen as a result of aneuploidy at the secondary level, followed by chromosome doubling. This, in fact, may be a more conservative and realistic explanation, and is especially to be suspected in such genera as *Typhonium*, *Biarum*, and *Cryptocoryne*, all with apparent heteroploid series (see Arends at al., 1982). In either case, chromosome numbers such as those discussed in the preceding paragraph must be regarded as advanced.

In summary, most chromosome counts in Araceae appear to be explainable on the dual basis of ascending and descending aneuploidy at the secondary (paleodiploid) level from a primitive base number of $x = 7$ (or perhaps 6), with subsequent (paleo)polyploidy in many cases. Ascending aneuploidy at the primary (paleodiploid) level, though it no doubt has occurred up to at least $x = 9$ and probably even $x = 11$ in a few cases, does not seem to merit the emphasis it has received, given that so many genera are still clearly based on multiples of seven. The most primitive extant chromosome numbers in Araceae are probably, on the one hand, those "paleodiploids" of members of the original paleoaneuploid series, i.e., $2n = (12)$, 14, 16, 18, and perhaps 20 and 22; and, on the other hand, "paleotetraploids" of the primitive base number, i.e., the widespread $2n = 28$ (or perhaps $2n = 24$, if $x = 6$ is accepted as primitive). Allotetraploids, secondary aneuploids, higher polyploids, and combinations of these would necessarily be more advanced. Allotetraploids based partly on $x = 7$ (or 6), i.e., $2n = 26$ and $2n = 30$, should be relatively more primitive than those involving higher base numbers, and so on.

More chromosome data are needed, and older reports need to be thoroughly reevaluated and reassessed, as Sheffer & Croat (1983) did for *Anthurium*, before anything close to a clear picture for chromosome number evolution in Araceae emerges.

Analyses of chromosome evolution and data on chromosome size for some individual aroid subtaxa are offered in Grayum (1984) and Petersen (1989). Aroid chromosomes range in length from about 1 μm (*Pistia stratiotes*) to at least 13.6 μm (*Zamioculcas*; Jones, 1957); most genera fall into the "medium" range (3–6 μm) of Ramachandran (1978). The phylogenetic significance of these data is as yet unclear.

PHYTOCHEMISTRY

Phylogenetically relevant phytochemical data for Araceae are found in Hegnauer (1963, 1986, 1987), Gibbs (1974), Dahlgren & Clifford (1982), and Grayum (1984). Data on useful characters are particularly sparse for this field, so no phytochemical characters were used in the character analysis undertaken during this study. Only the most basic and significant trends are recorded below.

Inorganic compounds. Silica bodies are unknown in Araceae (Dahlgren & Clifford, 1982). As discussed previously, calcium oxalate crystals occur throughout the family (Nicolson, 1959).

Carbohydrates. Polysaccharide mucilage is very abundant (and perhaps universal) in the Araceae, as in monocots in general (de Wildeman, 1942; Gibbs, 1974). Czaja (1978) studied the structure and properties of starch grains in vascular plants and divided Araceae into two seemingly artificial groups on this basis. Aroid starch grains were also studied by Reichert (1913; see summary in French, in press), although too few genera were examined to permit any significant generalizations.

Nitrogenous compounds. Amines are supposedly "common in the inflorescences of aroids" (Gibbs,

1974), although virtually all reports concern *Amorphophallus* and genera of the Arinae (*Sauromatum*, *Dracunculus*, *Arum*). Free indoles have also been reported from the same genera. All of these compounds appear to be concerned with the production of heat and stench associated with pollination by flies and carrion beetles (Chen & Meeuse, 1971) and ought to be expected in any genus exhibiting this syndrome.

Alkaloids are reported from a range of aroid genera (see Willaman & Li, 1970; Hegnauer, 1986) but have been identified in only a few cases.

Terpenoidal compounds. Volatile terpenoids (ethereal oils) are very uncommon in Araceae. Hegnauer (1963, 1986) reported that the dried rhizomes of the Old World species *Homalomena rubescens* and *H. aromatica* yield about 5% and 1.2% ethereal oil, respectively, apparently from the schizogenous (intercellular) ducts. New World species of *Homalomena* typically have highly aromatic foliage, rhizomes, and/or roots (pers. obs.).

El-Din (1968) identified a bicyclic monoterpene as the principal component of the floral odor in *Alocasia portei*, suggesting a role in attracting insect pollinators. It is possible that volatile terpenoids are more widespread in aroid inflorescences.

Triterpenoidal saponins are rather frequent in Araceae, as in many other monocots (Hegnauer, 1963; Gibbs, 1974; Grayum, 1984). Although these compounds are absent from many aroid genera, their distribution does not appear to be of systematic significance. The genus *Anthurium* contains both saponiferous and saponin-free species.

There are a few isolated reports of steroidal saponins in Araceae. Hegnauer (1963) regarded these as dubious.

Many authors have referred loosely to "resin" or "latex" in regard to araceous secretions, but until recently it was doubtful as to whether true polyterpenoidal resin or latex actually occurred in the family. Gibbs (1974) provided one report of "polyisoprenoids" in Araceae, from *Arum*. Most earlier authors (e.g., Trécul, 1866; Lierau, 1888; Krause, 1908; Solereder & Meyer, 1928; Hegnauer, 1963) described the contents of aroid "laticifers" as phenolic (i.e., tannins) rather than terpenoidal. However, French & Fox (manuscript) have now studied and characterized the apparently terpenoidal latex of various Araceae, and the contents of aroid resin canals are now known to be terpenoidal as well (French, 1987d).

French & Fox (manuscript) have investigated the ultrastructure of latex within the subfamily Colocasioideae and found it to be of systematic significance. They distinguished four types of particles, which they called S bodies, rubber particles, Y bodies, and R bodies. S bodies and rubber particles occur only in New World Colocasioideae and in the Old World genus *Hapaline*, whereas Y bodies are restricted to Old World genera except *Hapaline*. R bodies occur mainly in Old World genera. Fox & French (1988) found that sterol-esters are present in the latex of *Xanthosoma*, *Syngonium*, *Colocasia*, and *Alocasia*. However, free sterols occur only in latex of the former two genera, leading the authors to speculate that Old and New World Colocasioideae may be chemically distinguishable.

Phenolic compounds. Syringin is apparently not present in Araceae (Gibbs, 1974).

Flavonoids (including simple flavones, flavonols, anthocyanins, proanthocyanidins, flavone C-glycosides, and sulphated flavonoids) are "among the most valuable chemical markers for systematic purposes" (Harborne, 1982). Aroids are characterized by a predominance of flavone C-glycosides, abundant flavonols, and a comparative dearth of simple flavones. The predominance of flavone C-glycosides and the frequent presence of proanthocyanidins are construed as primitive conditions (Williams et al., 1981).

Anthocyanin pigments are not generally regarded as having great systematic value. In Araceae they occur in reddish fruits, some spathes and spadices, petioles, and in the epidermis of some leaf blades (Williams et al., 1981). Cyanidin 3-rutinoside is by far the most common form in Araceae, though several others are known. An unusual anthocyanin, the gentiobioside of pelargonidin and/or cyanidin, has been detected only in *Anchomanes* and *Cercestis* and is believed to indicate a close relationship between these genera (Williams et al., 1981).

The distribution of flavonols in Araceae is reported in Bate-Smith (1968), Williams et al. (1981), and Grayum (1984). Flavonols as a group occurred in only 27% of the species tested by Williams et al. (1981); they are frequent only in Engler's Colocasioideae, Philodendroideae, and Calloideae, and are the predominant flavonoids in leaves of the tribe Orontieae. Flavonols were not detected in Lasioideae, *Pistia*, or Aroideae except *Stylochaeton*, where they predominate in a manner "curiously similar" to the tribe Orontieae (Williams et al., 1981).

Flavone C-glycosides are "the most characteristic flavonoid constituents" of the Araceae and

were found in 82% of the species surveyed by Williams et al. (1981). The vast majority of species in all taxa except Monsteroideae and Orontieae contained these compounds.

Simple flavones are rare in Araceae, occurring in only 6% of the species examined (Williams et al., 1981). Though rare, flavones do seem to have some systematic value in Araceae in that they are concentrated in the subtribe Arinae. Luteolin and chrysoeriol both occur in this taxon, the former exclusively. Araceae lack the distinctive flavone tricin, so characteristic of palms, grasses, and Cyperaceae (Williams et al., 1981; Harborne, 1982).

Proanthocyanidins are "extremely widely present in leaves of monocotyledons and their almost universal occurrence robs them of any systematic significance" (Harborne, 1982). Moreover, their presence may be masked by anthocyanins, at least in Araceae, making them difficult to detect (Williams et al., 1981). Proanthocyanidins are widespread in Araceae but appear to be absent from Monsteroideae, Orontieae, and Aroideae (except *Stylochaeton* and the Arophyteae) (Williams et al., 1981).

Flavonoid sulphates appear to be rare in Araceae, having been identified in only a few, mostly unrelated genera (Williams et al., 1981).

Phenolic (cinnamic) acids (caffeic, p-coumaric, sinapic, and ferulic) are widespread in Araceae according to Bate-Smith's (1968) survey. They seem particularly rich in Monsteroideae and poorly represented in Aroideae, but beyond that no generalizations are possible. Harris & Hartley (1980) detected no phenolic acids bound to the cell walls of *Sauromatum* or *Pistia*.

Although leucoanthocyanidins have been alleged to be common in Araceae (Hegnauer, 1963), all records either pertain to weak or dubious reactions or are contradicted by negative or doubtful reports (see Grayum, 1984), with the exception of two mutually corroborating positive reports for *Philodendron*.

Tannins are frequently attributed to Araceae in the early literature (e.g., Trécul, 1866; Solereder & Meyer, 1928); however, it appears that only Gibbs (1974) has rigorously and systematically tested for them. According to his data, tannins are present in some genera and absent in others. The systematic significance of their distribution, if any, is not yet clear. *Anthurium* appears to have both tanniniferous and tannin-free species. According to Hegnauer (1963), aroid tannins are of the type derived from leucoanthocyanidins, so the widespread occurrence of the latter compound in Araceae is perhaps to be expected.

Cyanogenic glycosides. The Araceae are generally regarded as particularly rich in cyanogenic glycosides (Hegnauer, 1977; Dahlgren & Clifford, 1982). Only the tyrosine-derived glycoside triglochinin is known from Araceae (Nahrstedt, 1975). An enzyme is required to cleave off the cyanide from a cyanogenic glycoside (Hegnauer, 1977); the highly specific enzyme β-glucosidase has been isolated from *Alocasia macrorrhizon* (Hösel & Nahrstedt, 1975).

According to Nahrstedt (1975), cyanogenesis is known from all aroid subfamilies except Monsteroideae, Calloideae, and Pistioideae. The individual reports cited by Hegnauer (1963, 1986) and Gibbs (1974) tend to support this, although there are at least two positive reports for *Calla* and one for *Lysichiton*. Reports for many genera are contradictory, rendering all of the unreplicated reports dubious.

The distribution of cyanogenic and noncyanogenic genera in Araceae, according to the available laboratory data (see Grayum, 1984), does not appear phylogenetically significant. It is of interest, however, that crushed leaves of many Old World Colocasioideae yield a strong cyanide odor, whereas those of New World members of this subfamily do not. This test has been used in the field in Central America to separate the indigenous *Xanthosoma* from some widely naturalized species of *Alocasia* (B. E. Hammel, pers. comm., substantiated by pers. obs.). Laboratory data are not sufficient to provide a sound basis for these observations.

Phylogeny and Classification

Character Analysis

The possible phylogenetic (cladistic) relationships of the infrafamilial taxa in Araceae have been analyzed formally in the present study, with respect to the phenetic data assembled in the foregoing sections. Thirty-six characters were used in this analysis; these were selected for their apparent taxonomic value and also because they have been comparatively well surveyed in most cases. Characters not involved in the formal analysis have been considered and frequently brought into play in interpreting the often ambiguous implications of the cladistic analysis; the same is true for important characters that were discovered or surveyed after the analysis. The 36 principal characters used in the analysis are listed in Table 4.

Certain of Engler's infrafamilial taxa of various rank were accepted a priori as natural assemblages. These generally comprise genera, subtribes, and

tribes; in only one case (Pistioideae) has an entire Englerian subfamily been considered as a unit. The taxonomic units employed in the analysis are the same as those used for the headings in the following discussion, except where indicated. Each of these units was compared with every other unit for all of the characters in Table 4, and all shared derived characters (i.e., potential synapomorphies) were noted for each comparison. Presumed autapomorphies were not utilized; only the presumed most primitive condition of each character in a taxon was employed for analytical purposes. Similar autapomorphies of different taxa thought perhaps to reflect parallel tendencies are occasionally noted in the discussions.

Similar character analyses to that described above, employing fewer characters, have already been performed on Araceae by Howarth (1957) using mostly floral and embryological characters. Her analyses dealt with larger and more heterogeneous, sometimes artificial, taxa—Engler's subfamilies and Hutchinson's tribes—and yielded via a rather simple calculation a so-called "advancement index" for each taxon. Such an appraisal, though perhaps providing a more or less adequate phenetic evaluation indicating the approximate evolutionary grade of each taxon, says nothing about cladistic relationships.

For the record, Howarth's advancement indices for the eight Englerian subfamilies are as follows (higher numbers indicate greater phenetic "advancement," i.e., a smaller proportion of primitive character states): Monsteroideae 36%, Lasioideae 36%, Pothoideae 38%, Calloideae 42%, Aroideae 54%, Philodendroideae 75%, Colocasioideae 79%, and Pistioideae 86%. Howarth's advancement indices for Hutchinson's tribes are included in Appendix 1. These figures are sometimes more informative, since the taxonomic units involved are smaller and consequently more likely to be monophyletic.

The results of the character analysis undertaken in the present study are discussed under the following headings, as they pertain to aroid subtaxa accepted as monophyletic. The linear arrangement reflects the cladogram proposed at the end of this section. Since the discussions that follow incorporate much information presented in other parts of this paper, literature citations have frequently been omitted.

Gymnostachys. The monotypic or ditypic *Gymnostachys* is the only aroid genus endemic to Australia. Because of its narrowly linear leaves, *Gymnostachys* bears a superficial resemblance to *Acorus*, with which it has been closely aligned virtually since its discovery. There is not, however, good evidence that *Gymnostachys* is related to *Acorus*, nor that it should be dissociated from Araceae as the latter genus has been (see Grayum, 1987).

Gymnostachys is isolated (French & Kessler, 1989) and phenetically rather primitive and shares few derived characters with other aroid taxa. It has been rather poorly investigated, especially embryologically. Although there are some striking similarities to the tribe Orontieae (foliar prophylls; lack of ovular trichomes; lack of a spathe; gynoecial features similar to *Symplocarpus*), I believe that *Gymnostachys* is most closely related to the Potheae. The two taxa occur sympatrically and have similar patterns of anther endothecial thickening (French, 1985a); further, *Gymnostachys* is said to have $2n = 48$ chromosomes (J. Bogner, pers. comm.), an unusual number in Araceae but comparable to $2n = 24$, reported for species of *Pothos*. Thus *Gymnostachys* is here included as a tribe in subfamily Pothoideae.

Judging from its occurrence in tropical rainforests, where it grows alongside *Pothos* and *Alocasia*, it seems likely that *Gymnostachys* entered Australia via New Guinea from Laurasia subsequent to the collision of the Laurasian and Australian plates during the Miocene, about 10–12 myBP (Raven, 1979).

Potheae. The Potheae, comprising the genera *Pothos*, *Pothoidium*, and *Pedicellarum*, are a phenetically rather primitive tribe, with the lowest advancement index (23%) of any of Hutchinson's 18 tribes (Howarth, 1957). This is slightly exaggerated, however, due to Howarth's almost complete reliance upon floral characters. Vegetatively, the tribe is more specialized, made up of mostly monopodial climbers with geniculate petioles, distinctive (Pattern 3) stem vasculature, reticulate leaf venation, trichosclereids (at least sometimes), prisms, vessels in the stem, a cortical vascular system, and a stem endodermis. The Potheae, which are still poorly known cytologically and are unknown embryologically, are here treated as the sister group to Anthurieae.

All of the above character states are shared with at least some genera here considered to belong to the tribe Monstereae. Hence, the Potheae/Anthurieae are here placed in a sister group relationship with the Monstereae and satellite taxa, thus necessitating the union of Engler's subfamilies Pothoideae and Monsteroideae. Nicolson (1960b) and Hotta (1970) have already raised this possibility,

and Carvell (1989) endorses such a merger on floral-anatomical grounds.

Pedicellarum paiei is probably a species of *Pothos* sect. *Allopothos*. All of the character states on which *Pedicellarum* was founded have been shown in this paper to be misinterpreted (introrse anther dehiscence) or variable within the species (pedicellate flowers, fused perianth members). Fused and distinct perianth members both occur in *Pothos remotiflorus* of sect. *Allopothos* (Grayum, 1984; Nicolson, 1984a). Although I once (Grayum, 1984) proposed a new combination in *Pothos* for *Pedicellarum paiei*, recent information (Nicolson, 1984a; Carvell, 1989) suggests that *Pedicellarum* is better retained for now.

Zamioculcadeae. This isolated and bizarre African tribe of two genera (*Zamioculcas*, *Gonatopus*) shows every indication of being a remnant of a very old African flora. Since the group is so highly idiosyncratic, its relationship to other aroid taxa is difficult to fathom. The greatest phenetic resemblances, according to the present analysis, are with the tribes Spathicarpeae and Monstereae. With the former taxon (in which Hutchinson actually included *Gonatopus*), Zamioculcadeae share a tuberous growth habit, reticulate leaf venation, unisexual flowers, and the unusual base chromosome number of $x = 17$. However, details of floral morphology strongly suggest that monoecy in both groups is of relatively recent and independent derivation.

Zamioculcadeae are here treated as a sister group of Monstereae with which they share distichous, pinnate leaves, geniculate petioles, compound vascular bundles, and zonate, foveolate, starchy pollen. Fully pinnate to bi- or tripinnate leaves are unique to Zamioculcadeae; however, Monstereae exhibit the greatest tendency toward pinnation of any other aroid subgroup; furthermore, zonate pollen is restricted to these two tribes. There is little superficial resemblance between members of these taxa, although Zamioculcadeae must have been subjected to intensive selection pressure during the Neogene and Quaternary when the African flora was severely impoverished by widespread aridity (Raven & Axelrod, 1974).

Bogner & Nicolson (in press) transferred Zamioculcadeae to subfamily Lasioideae for unclear reasons. Floral anatomy, however, may provide some support for such an alliance (Carvell, 1989). The wide separation of *Gonatopus* from *Zamioculcas* and the juxtaposition of the latter with *Stylochaeton* and the Arophyteae, as proposed by Hutchinson (1973), are altogether indefensible from the standpoint of character analysis.

Anthurium. This huge neotropical genus is phenetically rather primitive in most respects and shares few derived characters with other aroid subtaxa. The greatest resemblance seems to be with Potheae, near which most authors have placed *Anthurium*. These taxa share geniculate petioles, reticulate venation, cortical vascular systems, stems with an endodermis, and similar or perhaps identical base chromosome numbers (apparently $x =$ 12 in *Pothos* and in sect. *Tetraspermium* of *Anthurium*, and possibly the entire genus; see Sheffer & Croat, 1983). Although the forate pollen of *Anthurium* is unique in Araceae, the commonly spinulose-reticulate exine of this genus finds its counterpart only in *Pothos* sect. *Allopothos* (see Grayum, in press a).

Although *Anthurium* and *Pothos* differ in several important respects, including growth habit, phyllotaxy, and flavonoid pattern (Williams et al., 1981), they appear more similar to one another than either is to any other taxon, and they are here treated as sister groups.

The di- or tritypic section *Polyphyllium* is unique within *Anthurium* in several important attributes (anisophyllous growth, internodal roots, inaperturate gemmate pollen, and other features), and may merit separate generic status.

The unrivaled diversity of *Anthurium* in southern Central America and the Andean region is probably related to the Andean orogeny (Gentry, 1982). The practically invariable pollen morphology of such diverse sections as *Pachyneurium* (Grayum, in press a) suggests a relatively recent adaptive radiation.

Spathiphylleae. The association of the oligotypic New Guinean genus *Holochlamys* with the polytypic, largely neotropical *Spathiphyllum* in a single tribe is now widely accepted (see Grayum, 1984). This was a matter of controversy for some time, following Hutchinson's ill-advised placement of *Holochlamys* in the tribe Lasieae.

The Spathiphylleae clearly belong to the Pothoideae (where *Spathiphyllum* has been assigned by all members of the Schottian school) or Monsteroideae (according to the Englerian school), as suggested by such characters as distichous leaves, geniculate petioles, possession of trichosclereids, absence of laticifers, and a thoroughly primitive floral plan (perhaps the most primitive in Araceae). The two subfamilies are combined in the present treatment (see discussion under Potheae). Vegetatively, the Spathiphylleae are less specialized than either the Potheae or Monstereae in having an acaulescent or rhizomatous growth habit and in

lacking prisms, vessels, a cortical vascular system in the stem, and a stem endodermis. Thus, Spathiphylleae are here considered the most cladistically primitive tribe of Pothoideae.

The most conspicuously derived feature of Spathiphylleae is its inaperturate, striate pollen, yet this is probably not homologous with similar pollen occurring in more phenetically advanced aroid taxa (see Grayum, in press a).

The Spathiphylleae are of great biogeographic interest (see especially Nicolson, 1968b; Williams & Dressler, 1976; Grayum, 1984). The contemporary occurrence of *Spathiphyllum* in Southeast Asia and in the Neotropics, and its absence from Africa, are probably best explained by a West Gondwanalandic origin followed by migration from Africa to Southeast Asia, and the subsequent extirpation of the African elements due to increased aridity during the Neogene and Quaternary. This hypothesis and the only other plausible one (see Grayum, 1984) suggest that *Spathiphyllum* sect. *Massowia* (which occurs in Southeast Asia and the New World) is artificial, as Williams & Dressler (1976) intimated.

Anadendrum. This distinctive Southeast Asian genus is largely unknown cytologically, embryologically, and anatomically. Its relationships are clearly with Pothoideae (Englerian school) or Monsteroideae (Schottian school). *Anadendrum* exhibits a combination of characters that argues strongly for merging these two subfamilies; since they have been merged in the present treatment (see discussion under Potheae), the decision of where to place *Anadendrum* is obviated.

Although it lacks trichosclereids, *Anadendrum* appears more closely related to Monstereae than to Potheae. For example, it exhibits intermittent diphyllous sympodial growth, which is otherwise known only from *Monstera* (Ray, 1988). Also, *Anadendrum* shows a tendency toward pinnatifid and even fenestrate leaves, uncommon in Araceae but characteristic of the former tribe. French & Tomlinson (1981b) reported that *Anadendrum* is much more similar in stem anatomy to certain Monstereae (especially *Amydrium*, the only member of the tribe without trichosclereids) than to Potheae. Five additional anatomical similarities of *Anadendrum* to Monstereae are provided in Nicolson (1984b, appendix 2). As in all Monstereae, the spathe in *Anadendrum* abscises cleanly following anthesis. The peculiar inaperturate, spinulose-pilate or spinulose-baculate pollen is out of place in either tribe.

Anadendrum is here provisionally regarded as a sister taxon to Monstereae/Zamioculcadeae.

Heteropsis. This small, neotropical genus combines monopodial growth and absence of trichosclereids, typical of Engler's subfamily Pothoideae, with inflorescence and floral features of Monsteroideae. The two subfamilies are combined in the present treatment (see under Potheae).

The strong floral-morphological resemblances between *Heteropsis* and Monstereae (Type II spathes that abscise immediately after anthesis; naked, bisexual, four-merous flowers; long, flat stamens) are augmented by the medium-sized, foveolate, starch-bearing, binucleate, zonate to diaperturate pollen common to the two taxa (see Grayum, in press a). *Heteropsis* is also more similar to Monstereae in floral anatomy (Carvell, 1989). Thus I agree with all members of the Schottian school in aligning *Heteropsis* with Monstereae, in which it is here included as a subtribe. Stem anatomy of *Heteropsis* is said to be more similar to that of Potheae (French & Tomlinson, 1981c), but this may reflect the similar and probably convergent growth habits of these taxa.

Monstereae. The eight (nine, if *Heteropsis* is included) genera of this pantropical tribe are strongly united vegetatively, florally, and palynologically. With a few exceptions (*Heteropsis*, *Amydrium*), Monstereae have been maintained intact by most prominent authors.

The Monstereae are here tentatively considered most closely related to the highly derived African tribe Zamioculcadeae. They are also clearly related to elements of Engler's subfamily Pothoideae, especially *Heteropsis* (here included within Monstereae), *Anadendrum*, and Potheae. The Spathiphylleae, treated by Engler as the sister group of Monstereae, are here considered more distantly related.

The Englerian subfamilies Pothoideae and Monsteroideae have been merged in the present paper because Engler's characterizations of the two taxa (Pothoideae with reticulate leaf venation and lacking trichosclereids, Monsteroideae with parallel venation and trichosclereids) do not circumscribe natural groups (see discussions under Potheae, *Anadendrum*, Spathiphylleae, and *Heteropsis*).

Relationships among genera within the Monstereae are not completely resolved. *Rhaphidophora*, *Epipremnum*, and *Monstera* are so poorly differentiated that their integrity as genera has been questioned (see, e.g., Bakhuizen van den Brink, 1958). Similarly, *Scindapsus* and *Alloschemone* have sometimes been united (Madison, 1976). *Rhodospatha* and *Stenospermation* share several unusual features and are probably sister genera (see Grayum, 1984).

Orontieae. Each of the three genera (*Lysichiton*, *Symplocarpus*, *Orontium*) of this tribe (formerly known as Symplocarpeae) were also considered individually in the present analysis. Phenetically, the group is quite primitive and shares few derived characters with other taxa. Features appearing to unite the Orontieae are homeophyllous sympodial growth, uniovulate locules, absence of endosperm, anomocytic stomata (occurring elsewhere only in *Pistia*), a base chromosome number of $x = 13$ or 14, a north temperate distribution, and a characteristic and unusual flavonoid profile (Williams et al., 1981). Thus the group appears to be natural.

Nonetheless, there appears to be a rather substantial rift in the Orontieae, which has widened ominously as a result of Ray's (1988) recent studies. *Orontium* differs markedly from the other two genera by having tetraphyllous growth, distichous phyllotaxy, laticifers, paired inflorescences, absence of a spathe, six-merous flowers, basal placentation, and a base chromosome number of $x = 13$. It is here accorded separate tribal status. The occurrence of laticifers in *Orontium*, which (along with their absence in *Lysichiton* and *Symplocarpus*) was verified by Rosendahl (1911) and French (1988), is especially perplexing and may reflect an independent derivation of this character state. *Orontium* is unknown embryologically and deserves highest priority (along with *Gymnostachys*) in this respect.

The relationship of the tribe Orontieae sensu lato to other taxa in Araceae is difficult to pin down, largely as a consequence of the dearth of advanced characters. The Lasieae are similar in most morphological respects and likewise have a base chromosome number of $x = 13$ or 14. Lindley (1847), Schott (1860), Hooker (1883), and Hutchinson (1973) all classified *Orontium* and/or *Symplocarpus* among lasioid elements. *Stylochaeton*, though with many advanced floral character states, has a number of primitive features (absence of laticifers; perigoniate flowers; elongate stamens; a base chromosome number of $x = 14$; and reticulate, boat-shaped, monosulcoidate pollen) and has a flavonoid profile remarkably similar to that of the Orontieae. These taxa are treated here as constituting subfamily Lasioideae.

Stylochaeton. Lindley (1847) placed the African genus *Stylochaeton* next to *Cryptocoryne* due to wholly superficial resemblances in spathe and spadix structure. Hutchinson included it with *Zamioculcas* and the Arophyteae for no conceivable reason other than that all three taxa are African. Because of its reticulate leaf venation and unisexual flowers, Engler (1920a) treated *Stylochaeton* as a monotypic tribe of the Aroideae.

All of these authors overlooked the fact that *Stylochaeton* is an isolated and phenetically primitive genus. Features primitive within Araceae include a rhizomatous habit; cordate/sagittate leaves; absence of laticifers (French, 1988); perigoniate flowers; plurilocular ovaries with multiovular axile placentation; elongate stamens with longitudinal anther dehiscence; anatropous ovules; presence of endosperm; a base chromosome number of $x = 14$; and boat-shaped, reticulate, binucleate and (at least in sect. *Spirogyne*) monosulcoidate pollen.

Most of the rather few advanced character states of *Stylochaeton* appear to represent autapomorphies and hence are not useful for classification. The Type IV spathe is constricted above the spadix rather than lower down as is typical for Araceae; monoecy is attended by such unusual features as perigoniate flowers and elongate stamens and pistillodes (in the male flowers), and has likewise certainly evolved independently. Starchy pollen is probably also independently derived in *Stylochaeton*, since all other genera with reticulate, boat-shaped pollen (except *Lysichiton*) have starchless pollen.

Stylochaeton cannot be included in any of the more "advanced" aroid subfamilies (Philodendroideae, Colocasioideae, or Aroideae), since it possesses none of the important synapomorphies characterizing these groups. Here it is placed, along with Lasieae and Orontieae, in the subfamily Lasioideae, as a monotypic tribe in which monoecy is considered to have evolved independently from the rest of the family (just as *Pycnospatha*, of the Lasieae, has independently acquired naked flowers). Stylochaetonieae have been treated as the sister group of Symplocarpeae, which also lack laticifers and have a strikingly similar flavonoid profile (Williams et al., 1981). Symplocarpeae differ in their north temperate distribution, parallel leaf venation (according to Ertl, 1932), and seeds lacking endosperm.

Lasieae. The composition of Engler's subfamily Lasioideae has emerged as one of the major shortcomings of his system. The two major tribes, the pantropical Lasieae (comprising eight to ten genera) and the paleotropical Thomsonieae, have apparently been grouped together solely on the basis of superficial vegetative similarities among some of their members. These tribes are actually separated by as profound a gulf as any two taxa in Araceae, as is well evidenced by Howarth's (1957)

advancement indices: 30% and 29% for Hutchinson's tribes Lasieae and Dracontieae, respectively (the latter including *Symplocarpus*), and 84% for his tribe Pythonieae (including *Zomicarpa*, *Zomicarpella*, and *Xenophya*).

Apart from general resemblances in habitat, about the only features shared by Lasieae and Thomsonieae are a base chromosome number of $x = 13$ or 14 (here considered plesiomorphic) and seeds lacking endosperm. The phenetically primitive Lasieae are basically rhizomatous, lack laticifers (French, 1988), and have bisexual, perigoniate (except *Pycnospatha*) flowers and monosulcate, reticulate, generally small, starchless, binucleate pollen grains; the exclusively tuberous Thomsonieae are laticiferous, have unisexual, naked flowers and inaperturate, basically striate, medium-sized to large, starchy, trinucleate pollen grains. All major aroid phylogenists other than those of the Englerian school (e.g., Lindley, 1847; Schott, 1860; Hooker, 1883; Hutchinson, 1973) have separated the two tribes widely, typically associating the Lasieae with the Orontieae and the Thomsonieae with subtribe Arinae or with tribe Zomicarpeae. These are substantially the same affinities indicated by the present analysis.

The neotropical genus *Dracontium* and the Southeast Asian *Pycnospatha* seem more advanced than the rest of the Lasieae in their tuberous habit, deeply compound leaves (of the same general type seen in *Amorphophallus* and *Anchomanes*), more advanced (Type III) spathes, and rather large pollen; *Pycnospatha* has completely lost the perigonium. These genera bear the closest superficial resemblance to the Thomsonieae, but clearly this is a case of convergent evolution, every bit as obvious and superficial as certain well known and long-accepted examples from the animal kingdom (e.g., New World and Old World porcupines, kangaroo rats, and jerboas).

Calla. It is not clear why Engler grouped *Calla* and the Orontieae in the same subfamily. The only characters of any consequence that the two taxa have in common are unilocular ovaries and north temperate distributions. Apart from these, none of the character states appearing to unite the three genera of Orontieae sensu lato are known from *Calla*, which differs strikingly in having anisophyllous growth, collateral bundles, naked flowers, multiovulate ovaries, numerous stamens per flower, endospermous seeds, a base chromosome number of $x = 18$, a markedly different flavonoid profile (Williams et al., 1981) and small, diaperturate pollen.

Lindley (1847), Schott (1860), Hooker (1883), and Hutchinson (1973) all grouped *Calla* with the Monstereae. The two taxa have a number of features in common: distichous leaves, parallel leaf venation, naked, bisexual flowers (an unusual combination in Araceae, otherwise known only in *Pycnospatha* of the Lasieae), and diaperturate pollen (unique to these two taxa). However, *Calla* differs from Monstereae in lacking a geniculum and tricho-sclereids and, most problematically, in possessing laticifers (as verified by Rosendahl, 1911, and French, 1988).

Calla shares the greatest number of derived features with *Nephthytis* and *Callopsis* (here included in the Philodendroideae): laticifers, Type II spathes, unilocular ovules with basal placentation, base chromosome number of $x = 18$ (with *Callopsis*, which was so named well before its chromosomes had been counted), and absence of a perigonium. The combination of laticifers and a base number of $x = 18$ is characteristic of subfamily Philodendroideae as here construed, to which *Calla* is thus provisionally assigned (as the cladistically most primitive member in light of its distichous leaves, bisexual flowers, and aperturate pollen). Hotta (1970) also included *Calla* in Philodendroideae.

An unfortunate nomenclatural consequence of including *Calla* in Philodendroideae (or any other subfamily except Aroideae) is the necessity of replacing the latter name with the earlier Calloideae (see Nicolson, 1984b). Clearly the classification of taxa should not be guided or influenced by such nomenclatural considerations; however, I have continued to use the name Philodendroideae throughout the narrative portion of this paper and in the tables (except Table 5) for conceptual reasons.

Culcasia. Engler placed this African genus in subfamily Pothoideae even though it is highly discordant there due to its advanced inflorescence and floral morphology: Type III (enclosing) spathe, Type II (monoecious) spadix, naked flowers, a single ovule per locule, prismatic stamens, and anthers dehiscing by apical pores. Engler was swayed by certain vegetative features in common with Pothoideae: distichous leaves, geniculate petioles and, especially, absence of laticifers (confirmed by French, 1988).

All authors of the Schottian school, on the other hand, have placed *Culcasia* next to *Cercestis* of Engler's subfamily Lasioideae (Schott, 1860; Hooker, 1883; Hutchinson, 1973). Like *Culcasia*, *Cercestis* is an African genus consisting largely of

climbers; the genera also share a similar bud trace organization (French & Tomlinson, 1981b), inaperturate starch-bearing pollen (Grayum, in press a), and the unusual base chromosome number of $x = 21$.

The idea of a close relationship between *Culcasia* and *Cercestis* now enjoys a wide consensus among aroid workers, even including those of the neo-Englerian school (e.g., Bogner & Nicolson, in press). But although the latter authors would retain both genera in the subfamily Lasioideae, there is now overwhelming evidence that *Culcasia* and *Cercestis* are intimately related with *Philodendron* and thus must be transferred to the Philodendroideae. This evidence, generated and assembled by J. C. French, is discussed under the next heading. Distichous leaves and geniculate petioles are both already known in Philodendroideae (from *Heteroaridarum* and *Anubias*, respectively), however the lack of laticifers in *Culcasia* is highly bothersome. According to Carvell (1989) the floral anatomy of *Culcasia* is unique, even within the context of Philodendroideae.

Homalomeninae, Schismatoglottidinae, Aglaonemateae, *Philodendron*, *Zantedeschia*, *Anubias*, *Dieffenbachia*. These taxa represent the "core" of the Philodendroideae inasmuch as they have been aligned together in this subfamily by most important authors and are so treated here. Although each was considered separately for the present analysis, their interrelationships are difficult to resolve and it is most convenient to discuss them together.

The seven taxa listed in the above heading are all fundamentally rhizomatous (except *Zantedeschia*?) and have spiral phyllotaxy; petioles lacking a geniculum (except *Anubias*); mostly simple, oblong to cordate or sagittate leaves with parallel venation; a ring of collenchyma in the outer cortex of the stem or petiole (except apparently *Anubias* and the Aglaonemateae); secretion files; biforines; advanced (Type III or IV) spathes; monoecious (Type II or III) spadices; naked flowers; plurilocular ovaries (except Schismatoglottidinae); numerous ovules per locule (except *Dieffenbachia* and Aglaonemateae); axile placentation (basically parietal in Aglaonemateae and Schismatoglottidinae); generally 2–4 stout stamens per male flower; anther dehiscence by apical pores (except *Anubias* and the Homalomeninae); anatropous ovules; endosperm (except *Dieffenbachia* and the Aglaonemateae); staminodia on the female flowers (except *Anubias* and *Philodendron*); and psilate, starchy pollen (foveolate in some *Dieffenbachia* species, starchless in *Anubias*).

Most of the exceptions in the above list can be considered autapomorphies within the group in question. Other presumed autapomorphies include homeophyllous growth (in many *Philodendron* species), compound vascular bundles (in *Dieffenbachia*), inflorescence sympodia (in *Dieffenbachia* and many *Philodendron*), connate stamens (in *Dieffenbachia* and *Anubias*), and trinucleate pollen (in *Dieffenbachia*, *Zantedeschia*, and the Aglaonemateae).

Philodendron, Homalomeninae, and Schismatoglottidinae have in common the possession of intercellular spaces and ducts in the ground tissues. This feature probably influenced Engler's decision to group these taxa into a single tribe, the Philodendreae (here disbanded); however, it also occurs in *Culcasia* and the Nephthytideae. Another character shared with the last-mentioned tribe is the possession of megaspore dyads, known only from *Dieffenbachia*, *Homalomena*, and *Nephthytis* (Grayum, in press b).

Cytologically, the "core" Philodendroideae are quite variable but show a conspicuous absence of multiples of seven, which are so common in the rest of Araceae and considered basic to the family. Schismatoglottidinae is based on $x = 12$ or 13; *Philodendron*, *Dieffenbachia*, and *Zantedeschia* on $x = 16$ or 17; Aglaonemateae and Homalomeninae on $x = 20$; and *Anubias* on $x = 24$ (see Grayum, 1984).

Although all of the "core" Philodendroideae are retained in the subfamily in the present treatment, the traditional Englerian subfamilial classification has been abandoned. Instead, the group has been broken into five informal "alliances," each of which includes an admixture of taxa formerly assigned to other subfamilies. These "alliances" have not been given formal taxonomic recognition since their composition is mostly tentative and highly subjective (the number of characters used in the analysis having been insufficient to resolve the group fully). I believe, however, that subfamily Philodendroideae as here circumscribed comes much closer to being a natural group than either of Engler's subfamilies Lasioideae and Aroideae, from which most of the new taxa were transferred.

The compositions of the five "alliances" as here presented are considerably different from those originally conceived (see Grayum, 1984). Extensive changes have been necessitated by an outpouring of new data from the laboratory of J. C. French, currently the most prolific researcher on

Araceae. In the case of Philodendroideae, these data (organized in French, 1987b, and Mayo, 1986) have now established the close relationship among *Philodendron*, Homalomeninae, and the African genera *Culcasia* and *Cercestis* (formerly of Engler's Pothoideae and Lasioideae, respectively). These taxa are unique in possessing resin canals in the roots (French, 1987b) and a sclerotic root hypodermis (French, 1987a). They share similar stem and stamen vasculature (French, 1986b) and extrafloral nectaries (J. C. French, pers. comm.), and all but Homalomeninae lack an anther endothecium (French, 1986a; all other Araceae have an endothecium). These four taxa here compose the "*Philodendron* alliance" (Homalomeninae being raised to tribal rank). *Cercestis* has been dissociated from *Nephthytis*, which lacks most of the above character states, and assigned to its own tribe, Cercestideae.

Explanations for most of the other four "alliances" can be found under other headings: the monotypic "*Calla* alliance" (see under *Calla*); the "*Nephthytis* alliance," comprising former members of Engler's subfamilies Lasioideae (*Nephthytis*, *Anchomanes* and *Pseudohydrosme*, *Montrichardia*) and Aroideae (*Callopsis*, most genera of Engler's Zomicarpeae); and the "*Peltandra* alliance," including *Peltandra* and *Typhonodorum*, Schismatoglottidinae (here raised to tribal status), and the tribe Arophyteae from Engler's Aroideae (see under those headings).

The "*Aglaonema* alliance" includes the Aglaonemateae, *Anubias*, *Zantedeschia*, *Dieffenbachia*, *Bognera*, and the tribe Spathicarpeae from Engler's Aroideae. This is an especially tentative, difficultly defined group consisting mainly of those "core" Philodendroideae that do not seem to belong in any other "alliance"; the inclusion of Spathicarpeae here is highly speculative. A more extensive character analysis will be required for these taxa to be placed more confidently.

The entire subfamily Philodendroideae is treated in this paper as a sister group to subfamily Pothoideae (including Engler's Monsteroideae). The combinations of character states found in such genera as *Calla* and *Culcasia* (see under those headings) strongly suggest that this is a proper alignment. Some important characters exclusive to members of Pothoideae and Philodendroideae are geniculate petioles, cork formation in the aerial roots, compound vascular bundles, collateral bundles, and prisms. (For more, see Grayum, 1984.)

Peltandra, Typhonodorum. The striking similarities between these genera were pointed out by Buchet (1939) but have been largely downplayed by later authors. The two genera, which were considered separately in the present analyses, are virtually identical in every important respect, sharing more derived characters than any other pair of taxa compared in the present study: sagittate leaves; stem endodermis (of the subtype individually surrounding the vascular bundles); secretion files; Type IV (constricting) spathe; monoecious spadix with sterile male flowers above and below the fertile male region; no perianth; unilocular, uniovulate or pauciovulate ovaries; parietal placentation; stout, connate stamens; apical anther dehiscence; orthotropous ovules; absence of endosperm; apparent base chromosome number of $x = 56$; staminodia in the female flowers; and starchy, trinucleate pollen.

Based on the above evidence, the monotypic, Madagascan genus *Typhonodorum* and the ditypic, North American *Peltandra* are here combined in the tribe Peltandreae. One might even argue that they be merged in the same genus; the only notable difference between the two genera is the fusion of the staminodia into synandrodia in *Peltandra*, and both fused and distinct staminodia are tolerated in the genus *Asterostigma*.

Lindley (1847) and Schott (1860) placed *Peltandra* and *Typhonodorum* among colocasioid elements on the basis of their similar leaf venation and connate stamens. Although the Peltandreae lack the secretion tubes characteristic of Colocasioideae, there are some similarities. The base chromosome number of Peltandreae ($x = 56$) is a multiple of seven, as in Colocasioideae (with $x = 14$) but unlike all "core" Philodendroideae. The colocasioid genus *Hapaline* especially resembles the Peltandreae in having sagittate leaves and in its gynoecial morphology, trinucleate pollen, and distribution of sterile male flowers. Yet all of these features may have been independently derived.

The Peltandreae are here considered closest to tribe Arophyteae and subtribe Schismatoglottidinae. The latter group shares with Peltandreae the unusual characteristic of a stem endodermis surrounding each vascular bundle individually and tends to have a similar distribution of sterile male flowers. Schismatoglottidinae differ from Peltandreae in having distinct stamens, endospermous seeds, binucleate pollen, and a base chromosome number of $x = 12$ or 13.

The unusual geographic disjunction of the two genera in Peltandreae may be explained according to the following scenario: the group must have

originated in tropical West Africa subsequent to its separation from South America, with *Peltandra* reaching North America via Eurasia and the North Atlantic route prior to the Eocene. Peltandreae were then presumably extirpated in their homeland as a result of increasing aridity, with *Typhonodorum* (having viviparous germination) reaching Madagascar.

Bognera. A consensus has now been reached among aroid workers that this very poorly known, monotypic South American genus, originally placed in the tribe Zomicarpeae (Madison, 1980), belongs among elements here included in the "*Aglaonema* alliance" of Philodendroideae (see Mayo, 1986; Bogner & Nicolson, in press). Character analysis indicates a close phenetic resemblance with the Madagascan tribe Arophyteae (of the "*Peltandra* alliance"); however, this is unconvincing since very few character states are known for *Bognera*. The genus is likewise similar to the polytypic South American genus *Dieffenbachia* (sharing a fused spathe and spadix, sterile male flowers between the fertile male and female regions, connate stamens, apical anther dehiscence, and large, basically psilate pollen). I feel that this is a much more likely relative, however Mayo (1986) implicates *Anubias*.

Zomicarpeae. This tribe consists of four monotypic or oligotypic South American genera. Only *Zomicarpa* is even moderately well known phenetically. *Ulearum* and *Filarum*, which were analyzed as a pair apart from *Zomicarpa*, are unknown cytologically and anatomically. *Zomicarpella* is virtually unknown in all respects, and was not included in the present analysis.

The Zomicarpeae were treated by both Schott (1860) and Engler (1920b) and his followers as belonging with elements of Engler's Aroideae—a standard repository in the latter system for taxa with unisexual flowers and reticulate leaf venation. In the present work they are included partly in the "*Nephthytis* alliance" of Philodendroideae, and partly (*Zomicarpa*) in the Colocasioideae.

Filarum and *Ulearum* strongly resemble the African genus *Callopsis* and, less so, *Nephthytis*. With *Callopsis* they share a rhizomatous habit, cordate leaves with reticulate venation, a simple spathe fused basally with the spadix, rather few female flowers, unilocular and uniovulate ovaries, basal placentation, anatropous ovules, 2–3 distinct stamens, and spinose pollen. It is, of course, necessary to hypothesize that the present ranges of these taxa represent the remnants of a once continuous West Gondwanalandic distribution.

Zomicarpa also shows significant similarities with *Callopsis* and *Nephthytis*, differing from them, as also from *Filarum* and *Ulearum*, in its subtuberous habit, compound leaves, Type IV (constricted) spathe, plurilocular ovaries, and transverse anther dehiscence. Whereas *Filarum* and *Ulearum* are obviously closely related to one another, *Zomicarpa* stands apart. In addition to the above characters, it differs in its endospermous seeds and Atlantic coastal (Bahian) distribution (*Filarum*, *Ulearum*, and *Zomicarpella* occur in western Amazonia or in the Andean foothills). Most disturbing, however, is the recent discovery (French, 1988) that *Zomicarpa* has secretion tubes, here considered a unique synapomorphy for the Colocasioideae. I have been prompted by this to transfer *Zomicarpa* into the latter subfamily as a monotypic tribe, even though another synapomorphy (synandria) is thereby lost. Secretion tubes have not been sought in the remaining three genera of Engler's Zomicarpeae, but I predict they will be absent. The latter genera are here provisionally inserted in the Callopsideae (Philodendroideae).

Arophyteae. This is a well-defined and wholly Madagascan tribe of three genera, none of which were known to Engler or earlier authors. Hutchinson (1973) classed them along with *Zamioculcas* in his heterogeneous tribe "Stylochitonieae," which he effectively employed as a trash-basket category for miscellaneous African taxa of dubious affinity. Bogner (1972, 1975, 1978) has treated the Arophyteae as a tribe within subfamily Aroideae.

The Arophyteae are florally, cytologically, and palynologically one of the most highly advanced of all aroid taxa. They are a bit more primitive vegetatively in having a rhizomatous habit and basically cordate leaves. The strongest resemblances of this tribe to the Aroideae are its orthotropous ovules and inaperturate, globose, spinose, starchy, trinucleate pollen. Many other characters of Arophyteae are discordant in this subfamily: seeds lacking endosperm, connate stamens, staminodia in the female flowers, fusion of the spathe and spadix, base chromosome number of $x = 18$, and tropical African distribution. With the exception of connate stamens, these features are also rare or unknown in Colocasioideae.

Arophyteae share the greatest number of derived characters with *Callopsis* and *Nephthytis*, on one hand, and *Peltandra* and *Typhonodorum*, on the other. All of these are here placed in subfam-

ily Philodendroideae. With the East African *Callopsis*, the Arophyteae share reticulate leaf venation, basal fusion of the spathe and spadix, basal placentation, spinose pollen, and the base chromosome number $x = 18$. They differ from *Callopsis* in having a Type III or IV spathe, connate stamens, staminodia in the female flowers, orthotropous ovules, seeds lacking endosperm, and trinucleate pollen. Except for staminodia, all of the latter may be regarded as advanced character states; whereas only lack of endosperm is shared with *Nephthytis*, all are shared with both *Typhonodorum* and *Peltandra*. Furthermore, the staminodia in *Peltandra* are fused into synandrodia, just as in the Arophyteae, which is a very rare feature otherwise known only in *Asterostigma* sect. *Rhopalostigma*.

Taken in conjunction with the Madagascan distribution of *Typhonodorum*, the above evidence strongly suggests that the Arophyteae have a sister group relationship with the tribe Peltandreae. The only significant difference between the two groups is their base chromosome numbers ($x = 18$ and 56, respectively).

Since Africa and Madagascar have apparently been separated since at least the mid-Cretaceous (Raven, 1979), the Arophyteae probably arrived at their present location via long-distance avian dispersal.

Spathicarpeae. These eight South American genera appear to form a cohesive and natural assemblage. *Spathantheum* and *Spathicarpa* stand somewhat apart in their total or partial fusion of spathe and spadix and dorsiventral segregation of male and female flowers; *Spathicarpa* differs further in having unilocular, uniovulate ovaries, basal placentation, and trinucleate pollen. Schott's (1860) and Hutchinson's (1973) separation of these genera into their own tribe does not appear warranted. *Spathantheum* effectively bridges the gap between *Spathicarpa* and the remaining six genera, the latter of which have many of their own autapomorphic features (Grayum, 1984).

Lindley (1847) and all Schottian authors have tended to group the Spathicarpeae (formerly known as Asterostigmateae) with philodendroid genera, particularly near *Dieffenbachia*. Hotta (1970) also followed this course. Engler (1920a), on the other hand, included the Spathicarpeae in his subfamily Aroideae, presumably on the basis of their reticulate leaf venation. According to the character analysis performed here, the Spathicarpeae show a definite correspondence to members of the Philodendroideae, especially *Dieffenbachia*, and no compelling link to Aroideae. Mayo (1986) suggests a connection with the Arophyteae, also here included in Philodendroideae.

Some of the more prominent putative synapomorphies of the Spathicarpeae with members of the Philodendroideae are secretion files (French, 1988); a collenchyma ring in the outer cortex of the stem or petiole (exclusive to these two taxa); a base chromosome number of $x = 17$ (as in *Dieffenbachia* and *Philodendron*; cf. also Zamioculcadeae); and inaperturate, boat-shaped, verrucate to psilate, starchy, binucleate pollen virtually indistinguishable from that of *Philodendron* and *Homalomena*. With *Dieffenbachia*, the Spathicarpeae also share *Alocasia* type hydathodes (Müller, 1919), basal fusion of the spathe and spadix, connate stamens, and distinct staminodia in the female flowers (the latter two characters in combination being highly unusual in Araceae). The compound leaves of some genera of Spathicarpeae are very similar to those of certain *Philodendron* species, e.g., in sect. *Schizophyllum*.

The Spathicarpeae have here tentatively been included next to *Dieffenbachia* in the "*Aglaonema* alliance" of subfamily Philodendroideae. But although the tribe exhibits many specializations (tuberous growth habit, spiral phyllotaxy, compound leaves with reticulate venation, monoecy, fusion of the spathe and spadix, and connate stamens), it is in many respects phenetically more primitive than the other members of this assemblage. The spathe is generally of a rather simple type; even in *Spathicarpa*, it is flat, narrow and greenish. The spadix is basically of the most primitive monoecious type, i.e., with bisexual flowers still present between the male and female regions. The ovary is basically plurilocular, with axile placentation, and the stamens, though usually more or less connate, are mostly elongate and with longitudinally dehiscent anthers. Ovules are anatropous, and the seeds retain endosperm. The pollen of *Gorgonidium vargasii* is subreticulate and appears monosulcoidate (see Grayum, in press a). It is thus likely that monoecy has evolved independently and relatively recently in Spathicarpeae, as in Zamioculcadeae and *Stylochaeton*.

The distribution of the Spathicarpeae is also "primitive." The eight genera are restricted to the fringe of Amazonia from the Bahia coast of Brazil through the subtropical and warm temperate regions of northern Argentina, Paraguay, Bolivia, and southern Brazil, and northward along the Andean chain. This distribution more or less parallels

that of the tribes Lasieae and Zomicarpeae in South America and probably represents the vestige of a once more expansive range that has been reduced by vicariance events.

Nephthytis and *Cercestis*. These two African genera, generally placed together in the tribe Nephthytideae, were considered separately for the present analysis. The Nephthytideae were treated among philodendroid genera by Schott (1860), Hooker (1883), and Hutchinson (1973); however, Engler (1911) included them in his subfamily Lasioideae, apparently because of their reticulate leaf venation. According to the character analysis performed for this study, the tribe clearly belongs in Philodendroideae (see under Homalomeninae, etc.).

Character states of Nephthytideae considered synapomorphic with members of the Philodendroideae include monoecy, naked flowers, unilocular uniovulate ovaries with basal placentation, prismatic stamens with poricidal anther dehiscence, seeds lacking endosperm, a base chromosome number of $x = 20$ or 21, and inaperturate, boat-shaped, verrucate to psilate, starchy, binucleate pollen. These similarities are shared to the greatest extent with *Montrichardia*, *Callopsis*, *Anchomanes* and *Pseudohydrosme*, the Zomicarpeae, *Culcasia*, the Aglaonemateae, *Peltandra*, and *Typhonodorum*. The first five taxa in this list have been included with *Nephthytis* in the "*Nephthytis* alliance" of Philodendroideae (see under the appropriate headings for further details).

Cercestis comprises mainly scandent species based on $x = 21$. Although species of *Nephthytis* are rhizomatous and based on $x = 20$, the original character analysis did not reveal any major discontinuity between the two genera. Recently generated anatomical data, however, strongly suggest that *Cercestis* is much more closely related to *Culcasia* (also consisting largely of scandent species based on $x = 21$) than to *Nephthytis*, and that the former two genera are more properly associated with *Philodendron* and the Homalomeninae (see under Homalomeninae, etc.). Thus *Cercestis* has hereby been removed from the Nephthytideae to its own tribe, Cercestideae, which, along with the monotypic Culcasieae, is transferred to the "*Philodendron* alliance." The Nephthytideae have subsequently been enlarged to accommodate *Anchomanes* and *Pseudohydrosme* (see next heading).

Anchomanes and *Pseudohydrosme*. Schott (1860), Hooker (1883), and Engler (1911) agreed in placing these two African genera among lasioid elements in or near the tribe Thomsonieae. Hutchinson (1973), however, classed them in his tribe Richardieae, which consisted largely of philodendroid elements. Bogner & Nicolson (in press) essentially agreed with this alignment, including *Anchomanes* and *Pseudohydrosme* in the Nephthytideae (which, however, they retained in Lasioideae). Character analysis supports the latter position.

The resemblances of these two genera to the Thomsonieae are striking but superficial: tuberous stems; few or solitary large, compound leaves; and reticulate venation. This type of growth habit is common in Araceae and has evolved independently in several more or less unrelated lines, e.g., Zamioculcadeae, Spathicarpeae, Arinae, Lasieae, Zomicarpeae, and Colocasioideae (*Chlorospatha*). The compound leaves of *Anchomanes* and *Pseudohydrosme* differ in detail from those of Thomsonieae and appear to develop via the necrotic process as in Monstereae rather than the marginal process typical of Thomsonieae (see Riedl, 1978).

Anchomanes and *Pseudohydrosme* share a few apomorphic floral characters with Thomsonieae (naked flowers, uniovulate locules, seeds lacking endosperm), but these are just as characteristic of, say, Aglaonemateae. The following features of these genera appear to place them squarely in the Philodendroideae: Type II spadix, absence of sterile flowers (typical of *Montrichardia*, *Nephthytis*, etc.; unknown in Thomsonieae); a base chromosome number of $x = 20$ (common in Philodendroideae; Thomsonieae are based on $x = 13$ or 14); psilate, binucleate pollen (characteristic of Philodendroideae; pollen of Thomsonieae is basically striate and uniformly trinucleate); and a rare anthocyanin detected in *Anchomanes* and otherwise known only from *Cercestis* (Williams et al., 1981).

I now follow Bogner & Nicolson (in press) in placing *Anchomanes* and *Pseudohydrosme* directly into the Nephthytideae (I had previously segregated them in their own tribe; Grayum, 1984). These taxa apparently have the same base chromosome number, $x = 20$ (*Pseudohydrosme* is yet unknown cytologically), and differ principally in leaf architecture. However, sagittate and highly compound leaves occur together in several other tribes and even subtribes (Spathicarpeae, Dracontiinae, Arinae, and others). *Anchomanes* has aculeate petioles (unknown in Thomsonieae), a condition which is also occasionally seen in *Nephthytis afzelii* (J. Bogner, pers. comm.).

Although *Pseudohydrosme* has two species, only *P. gabunensis* was included in the analysis. The second species, *P. buettneri*, is still unknown in

most respects. Florally it diverges markedly from *P. gabunensis* in having very different stamens and sterile male flowers at the apex of the spadix. It may be that this small genus is artificial.

Montrichardia. The tritypic neotropical genus *Montrichardia* shows strong similarities with genera here considered philodendroid and few similarities with the mainstream of Engler's Lasioideae (Lasieae and Thomsonieae). The closest relatives of the genus appear to be the African genera *Nephthytis* and *Anchomanes/Pseudohydrosme*, as recognized by most previous authors. *Montrichardia* is placed along with those taxa in the "*Nephthytis* alliance" of Philodendroideae in the present work.

The general resemblances among taxa of the "*Nephthytis* alliance" are listed under *Nephthytis* and *Cercestis*. The prickly trunk of *Montrichardia* recalls the aculeate petioles of *Anchomanes*, and its large, psilate, thin-walled, binucleate pollen is very similar to pollen of *Anchomanes* and *Pseudohydrosme*. The common ancestor of these taxa was presumably widespread across West Gondwanaland before that continent was bisected.

Montrichardia is still unknown chromosomally, but I predict it to have $2n = 36$, 40, or 42 chromosomes.

Callopsis. Engler treated this monotypic East African genus as a separate tribe in his subfamily Aroideae; Hutchinson grouped it with his tribe Colocasieae. Character analysis suggests that *Callopsis* is most closely related to taxa here composing the "*Nephthytis* alliance" of subfamily Philodendroideae, particularly to *Nephthytis* (see under *Nephthytis* and *Cercestis* for shared characteristics of this group). Noteworthy points of agreement with the neotropical genera *Filarum* and *Ulearum*, also of this "alliance" and here included in the Callopsideae, are discussed under Zomicarpeae. *Callopsis* also has a few features in common with the Madagascan tribe Arophyteae of the "*Peltandra* alliance."

Colocasioideae. The following subtaxa of Colocasioideae were analyzed separately: *Jasarum*, *Scaphispatha*, *Chlorospatha*, *Caladium/Xanthosoma/Aphyllarum*, Caladiinae, *Syngonium*, *Steudnera*, *Remusatia/Gonatanthus*, *Hapaline*, *Colocasia*, and *Alocasia*. The subfamily is here discussed as a unit for purposes of convenience.

The treatment of subfamily Colocasioideae looms as the most serious unresolved problem in the classification presented in this paper. On the one hand, this subfamily (it is accepted here virtually as circumscribed by Engler) is probably the most easily recognized of all aroid subfamilies. Moreover, the similarities among the various subtaxa are not superficial; the Colocasioideae are unified by an unusual number of apomorphic character states: most have a tuberous growth habit, basically sagittate to cordate leaves with a peculiar type of venation, secretion tubes (unique to this subfamily), Type IV (constricted) spathes, monoecious spadices with sterile flowers below the fertile male portion, naked flowers, connate stamens (but see *Zomicarpa*) with poricidal anther dehiscence, a base chromosome number of $x = 13$ or 14, and inaperturate, basically starchy pollen. Peltate leaves are widespread in Colocasioideae and almost unique here (occurring otherwise only in *Ariopsis*, *Homalomena*, and a single species each of *Anthurium*, *Pinellia*, and *Philodendron*).

On the other hand, there are some disturbing indications that the Colocasioideae may be diphyletic. And diphyletic or not, it seems possible that Colocasioideae may be derived from within some other subfamily or subfamilies, which would thus render the latter group(s) paraphyletic and argue strongly that Colocasioideae be submerged.

Subfamily Colocasioideae is provisionally kept together in this paper (except for *Ariopsis*). The following observations are pertinent to classification within the subfamily. Although not reflected in other classifications, there appears to be a deep and fundamental division in the subfamily roughly along geographic lines. The New World Colocasioideae differ in several important respects from the Old World members of the subfamily. Pedately compound leaves, for example, occur exclusively in New World Colocasioideae (but see also *Protarum*), where they are widespread; a cortical vascular system is found in most New World Colocasioideae but never in Old World members (French & Tomlinson, 1983); New World Colocasioideae differ markedly from all Old World genera except *Hapaline* in the color and detailed ultrastructure of their latex (French & Fox, manuscript), and preliminary data (Fox & French, 1988) suggest a chemical difference in the latex as well (although critical genera such as *Hapaline*, *Protarum*, and *Scaphispatha* were not studied); and there is some indication that cyanogenesis is limited to the Old World Colocasioideae.

Pollen morphology is also very different in the two groups. Old World Colocasioideae most frequently have spinose pollen, but it is clear that the most primitive exine sculpturing in this group is

striate (as in *Steudnera*, *Protarum*, and some species of *Colocasia*; see Grayum, in press a). Striate pollen is also the primitive type in Thomsonieae, and it occurs in other members of Aroideae. New World Colocasioideae most frequently have psilate pollen, consistent with pollination by dynastine scarab beetles, which is the rule among these taxa; only a few species of *Syngonium* (which may be bee pollinated) are known to have spinose pollen (see also *Zomicarpa*). The most primitive exine sculpturing in the New World taxa is reticulate (as in *Jasarum* and some species of *Chlorospatha*), which is also the case for Philodendroideae. Reticulate pollen is considered antecedent to striate pollen in Araceae (Grayum, in press a); thus, if the Colocasioideae are indeed monophyletic, the striate pollen of Old World members must have evolved independently of striate pollen in other Araceae.

It is conceivable that all of the above differences reflect the long isolation of the two segments of the subfamily following the breakup of West Gondwanaland; however, the same phenomenon is not evident between New and Old World members of other araceous taxa with presumably the same biogeographic history. I entertain the hypothesis that the New World Colocasioideae are related to or derived from the Philodendroideae, and the Old World Colocasioideae are related to the Aroideae. *Dieffenbachia* shows parallels with New World Colocasioideae, particularly *Chlorospatha* and *Syngonium*, with which it shares unusual pollen features (Grayum, 1984, in press a). A separate cortical vascular system occurs in *Philodendron*, *Dieffenbachia*, and New World Colocasioideae.

On the other hand, starch grains of the Old World genus *Colocasia* are of the "*Arum* type" and do not resemble those of *Peltandra* or *Dieffenbachia* (Reichert, 1913). The genus *Protarum* is in some respects intermediate between Aroideae (where Engler placed it) and Old World Colocasioideae.

The present evidence for diphylesis does not seem to outweigh the imposing list of putative synapomorphies appearing to unite the Colocasioideae. Moreover, recent work involving restriction fragment analysis of chloroplast DNA, while supporting the division of Colocasioideae into two tribes along hemispheric lines and (apparently) the ouster of *Ariopsis*, suggests that the subfamily is indeed monophyletic (Kessler & French, 1989). Thus I have opted for the conservative approach of maintaining Colocasioideae essentially in the Englerian sense. The only changes in content involve the exclusion of *Ariopsis* (transferred to Aroideae) and the inclusion of *Protarum* and *Zomicarpa* (transferred from Aroideae). However, character analysis strongly indicates sweeping changes in the internal classification of the subfamily.

Engler & Krause (1920) divided the Colocasioideae into three tribes: the monotypic Syngonieae and Ariopsideae, plus an all-inclusive Colocasieae. This scheme is both unilluminating and highly artificial. In the present work the bulk of the subfamily is divided into two coordinate tribes, the Colocasieae (consisting entirely of Old World genera) and the Caladieae (predominantly of New World genera), to reflect the differences discussed above.

Within the Old World tribe Colocasieae, Engler's subtribe Steudnerinae is clearly artificial on the basis of floral and pollen characters. *Steudnera* differs greatly from the other two genera in its small, boat-shaped, striate, binucleate pollen. In this sense it resembles *Protarum* and some species of *Colocasia* (Grayum, in press a); however, *Steudnera* is so distinctive in its Type II spathe and lack of sterile male flowers that it clearly deserves separate subtribal status.

Remusatia and *Gonatanthus*, on the other hand, are so similar morphologically and palynologically that they probably ought to be combined. These genera lack a sterile apical appendage on the spadix and have trinucleate pollen. I include them in a separate subtribe (Remusatiinae) from *Colocasia* and *Alocasia* (Colocasiinae), which have a naked apical appendage and binucleate pollen (with the exception of *Colocasia esculenta*).

The Colocasieae include the highly aberrant genus *Protarum*.

In the New World tribe Caladieae, *Jasarum*, *Scaphispatha*, and *Syngonium* stand out so much vegetatively, florally, cytologically, and/or palynologically that they all deserve subtribal status: *Jasarum*, by virtue of its Guayana Shield distribution, rhizomatous, aquatic habit, linear-lanceolate leaves, absence of a cortical vascular system, unilocular biovulate ovaries, basal placentation, seeds lacking endosperm (Bogner, 1985a), base chromosome number of $x = 11$, and fully reticulate pollen; *Scaphispatha*, in its primitive spadix (lacking sterile flowers), unilocular ovaries with basal placentation and unique exine sculpturing; and *Syngonium* in its vining habit, uniovulate locules, connate gynoecia, and absence of endosperm.

Scaphispatha is a still poorly known genus that Engler originally included in Aroideae. It is the only genus of Colocasioideae other than the Asian *Steudnera* to lack sterile flowers on the spadix.

The pollen, though unique in Araceae, is most nearly comparable to certain striate-derived types of Old World species (*Colocasia gigantea*, *Amorphophallus konjac*; see Grayum, in press a). Thus it is conceivable that *Scaphispatha* will prove to be a member of Colocasieae.

Zomicarpa, here considered a colocasioid due to its secretion tubes (French, 1988), has been kept in a separate tribe to emphasize its uniqueness in having distinct stamens. This New World genus shows some interesting similarities to *Pinellia* and *Arisaema*, of the Aroideae (Grayum, 1984). Its classification must still be considered highly speculative.

The remaining New World Colocasioideae, *Caladium*, *Chlorospatha*, *Xanthosoma*, and *Aphyllarum*, are probably best treated as a single subtribe, Caladiinae. *Syngonium* is much closer to the Caladiinae than to either *Jasarum* or *Scaphispatha*. Mayo & Bogner (1988) presented compelling evidence that *Aphyllarum* should be submerged in *Caladium*, but stopped short of formally effecting the reduction.

Remaining to be discussed is the enigmatic Southeast Asian genus *Hapaline*. This is, in many ways, the most phenetically advanced Old World colocasioid genus. It is distinctive in its nonpeltate leaves, fusion of spathe and spadix, uniovulate ovaries, base chromosome number of $x = 13$ (rather than $x = 14$), and trinucleate pollen (also in *Remusatia*). All of these features occur in the genus *Pinellia* (of Aroideae), to which *Hapaline* shows the greatest phenetic similarity. *Hapaline* is also unique among the Colocasioideae in having sterile male flowers above and below the fertile male region; this is characteristic of *Peltandra* and *Typhonodorum*, which *Hapaline* resembles in other respects. But since *Hapaline* has now been shown definitely to have secretion tubes (French & Fox, manuscript), its membership in Colocasioideae is virtually assured. The placement of *Hapaline* within the subfamily remains problematical. *Hapaline*, unlike all other Old World Colocasioideae, secretes a milky, white latex from its laticifers. Moreover, microscopic examination of this latex reveals that it is in every detail (presence of S bodies and rubber particles, and absence of Y and R bodies) exactly like that of New World genera (French & Fox, manuscript). And although *Hapaline* does not exhibit a well-defined cortical vascular system (typical of New World Colocasioideae), there is a "reticulum of laticifers" in the stem cortex with which "a more detailed study might reveal a reduced vascular system" in association (French, in press).

The pollen of *Hapaline* is of a derived type (globose, spinose, trinucleate) occurring in Colocasioideae of both hemispheres. Nonpeltate leaves are more characteristic of New World Colocasioideae, and fusion of the spathe and spadix is otherwise known only in the neotropical genus *Chlorospatha* (Grayum, 1984).

I here treat *Hapaline* as a subtribe in the otherwise New World tribe Caladieae, entirely on the basis of the above latex characters, which constitute the best evidence currently available. This decision entails the implication that the tribes Colocasieae and Caladieae must have diverged prior to the breakup of West Gondwanaland (still assuming that Colocasioideae are monophyletic) and clears the path for *Scaphispatha* (and possibly *Zomicarpa*) to be transferred to Colocasieae should that prove necessary.

The cladistic alignment of subfamily Colocasioideae, when considered as a monophyletic unit, is difficult to interpret. I have rather unconfidently derived the group from Philodendroideae. The Caladieae are more primitive than the Colocasieae in having basically reticulate pollen and, as previously discussed, they show certain similarities with members of the Philodendroideae. Furthermore, all of the apomorphic characters uniting the Colocasioideae also occur in one genus or another of Philodendroideae (Grayum, 1984). *Typhonodorum* and *Peltandra* have strikingly colocasioid venation and have even been included in Colocasioideae, though they lack secretion tubes (probably the most important synapomorphy for the subfamily). The distinctive gorgonoid type of inflorescence sympodium occurs only in Philodendroideae and Colocasioideae (Ray, 1988) and, according to French (1986c), orthotropous ovules occurring in Colocasioideae are more similar in detail to those of Philodendroideae than of Aroideae.

Derivation of Colocasioideae from within Philodendroideae would render the latter group paraphyletic, thereby suggesting that Colocasioideae ought to be submerged. Although there is a precedent for this (Colocasioideae were included in their entirety in Philodendroideae by Hotta, 1970), I prefer to maintain this distinctive and well-known subfamily for as long as the cladistic evidence for submerging and/or dividing it remains equivocal.

Protarum. Engler (1920a) treated the monotypic genus *Protarum* as a separate tribe of subfamily Aroideae. Hutchinson (1973) treated it as an integral part of the tribe Areae. *Protarum*

agrees with Aroideae (including Thomsonieae) in its tuberous habit, pedately compound leaves, advanced (constricted) spathe, naked apical spadix appendage, unilocular ovaries, orthotropous ovules, base chromosome number of $x = 14$ and, striate pollen.

Character analysis, however, indicates that Bogner & Nicolson (in press) were correct in transferring *Protarum* to the Colocasioideae. In the first place, all of the above character states also occur in and are in most cases basic to the Old World Colocasioideae, except for pedate leaves, which are widespread in New World Colocasioideae. *Protarum* has fully connate stamens, as do all Colocasioideae (but extremely few Aroideae). Furthermore, the striate pollen of *Protarum* is, in terms of its small size and peculiar pattern of striation, much more similar to that of *Steudnera* than to the pollen of any Aroideae (Grayum, in press a). And French (1988) has recently confirmed the presence of secretion tubes in *Protarum*.

Protarum is the only aroid genus endemic to, or even occurring in, the Seychelles Islands. Since the genus is phenetically distinctive and taxonomically isolated, recent long-distance dispersal to these islands can be ruled out. The Seychelles are believed to represent continental fragments of the Indian Plate, from which they are thought to have separated about 70 myBP—at about the same time India commenced its northward movement (Raven, 1979). *Protarum* probably reached the Seychelles via overseas dispersal from Africa or Madagascar, at some point after the separation of those islands from the Indian Plate (see Grayum, 1984). The Colocasioideae were then presumably extirpated or driven out of mainland Africa due to increased aridity (only the widespread and highly vagile *Remusatia vivipara*, which is certainly a very recent invader, occurs there today).

Arinae. The eight genera composing the Englerian subtribe Arinae represent the "core" of the subfamily Aroideae. The group has been classed together by all authors at least since the time of Lindley (1847), although frequently with an admixture of other more or less distantly related taxa.

The Arinae are held together by having a tuberous habit; basically sagittate leaves that often become compound; reticulate venation; secretion files; advanced, frequently constricted spathes; monoecious spadices with sterile flowers and/or naked regions above and below the fertile male portion; unilocular multiovulate ovaries with basically parietal placentation; mostly stout, distinct stamens; orthotropous ovules; seeds with endosperm; a base chromosome number of $x = 14$ (or perhaps $x = 7$); simple flavones (particularly luteolin, unique to this taxon); onagrad embryogeny; inaperturate, globose, spinose or spinose-reticulate pollen that is mostly starchy (except *Arum*) and trinucleate (with the possible exception of *Theriophonum*); and perigonia absent.

Few subtaxa of Araceae are defined by more synapomorphies than this one; yet the relationship of Arinae to the rest of the family is less clear-cut. The closest overall phenetic resemblances are shown by *Ariopsis* and *Arisaema*, the latter of which is here regarded as the sister taxon to Arinae. These genera agree in their tuberous habit, reticulate venation, secretion files, naked flowers, unilocular multiovulate ovaries, orthotropous ovules, seeds with endosperm, base chromosome number of $x = 14$, and inaperturate, globose, spinose pollen. *Arisaema* further agrees in having compound leaves, a naked spadix appendage, and starchy pollen; *Ariopsis* agrees in its parietal placentation and trinucleate pollen.

Lindley (1847) and Schott (1860) placed the Arinae in close juxtaposition with tribe Thomsonieae of Engler's subfamily Lasioideae. There is no question that Thomsonieae are completely out of place in Lasioideae (see discussion under Lasieae); they indeed agree well with Arinae and are here included with that group in subfamily Aroideae. Thomsonieae and Arinae share the following features: tuberous growth habits; compound leaves (in most Arinae); paracytic stomata; *Philodendron*-type hydathodes; reticulate venation; secretion files; advanced (Type III or IV) spathes; monoecious spadices with a sterile and usually naked terminal appendage; basically distinct stamens; a base chromosome number of $x = 13$ or 14; inaperturate, starchy, trinucleate pollen; similar starch grain structure (Reichert, 1913); and production of amines and free indoles in the inflorescence at anthesis.

The Thomsonieae differ from Arinae in having an altogether more primitive gynoecial structure (plurilocular ovaries with axile placentation, and anatropous ovules), seeds with endosperm, and basically boat-shaped, striate or striate-reticulate pollen (which, however, occurs elsewhere in Aroideae). But the number of apomorphies shared by Thomsonieae with Arinae far surpasses those few shared with Lasieae.

The geographic distribution of the Arinae is Tethyan, from Great Britain (*Arum*) and the Canary Islands (*Dracunculus*) through the Mediterranean region eastward to the Himalayan region and Central Asia (*Eminium*) and on to the Far

East, New Guinea, and Australia (*Typhonium*). It is probable that the group originated in the homogeneous flora that stretched along the northern margin of the Tethys Sea from western Europe to Indomalaya during the Eocene (Wolfe, 1975) and that it has only recently extended into tropical Africa (*Sauromatum venosum*) and Australasia.

Engler's tribe Areae is a sprawling, uninformative, and partly artificial assemblage comparable to his tribe Colocasieae, and the former tribe is here reduced to coincide with his subtribe Arinae. Most of the other former subtribes of Areae have been raised to tribal rank to emphasize their distinctiveness and isolation.

Arisaema. The closest outgroup to *Arisaema*, as discussed under the previous heading, is probably the Arinae. *Arisaema* has been placed fairly near Arinae by all important authors and does not differ from Arinae in many important respects: lack of sterile flowers below the fertile male region, basal rather than parietal placentation, usually more or less connate stamens, absence of luteolin, and binucleate pollen. *Arisaema* also shows a resemblance to *Ariopsis* (see under Arinae), especially in gynoecial and pollen characters, but differs markedly in leaf morphology and spadix structure. It shows some similarities to the neotropical genus *Zomicarpa* as well (tuberous habit, compound leaves, similar gynoecial structure, constriction of the spathe between the fertile male and sterile apical portions).

Arisaema has perhaps the widest distribution of any aroid genus: from central Africa and the Arabian Peninsula through south and east Asia and into North America as far south as Mexico. All 10–11 sections of the genus and 61 of the 150 or so species occur in the Himalayan region, according to Li (1980), who believes the genus originated there. This is probable since none of the outlying portions of the range (Africa, Southeast Asia, or North America) has a single endemic section. Furthermore, the most phenetically primitive section (the monotypic *Dochafa*, with male and female flowers on the same spadix) ranges from the Himalayan region west to Yemen. The adaptive radiation in *Arisaema* must have been relatively recent, however, in view of the vague separation among sections and the almost invariable pollen morphology throughout the genus, and likely owes to the new habitats made available during the uplift of the Himalayas, beginning with the collision of the Indian and Laurasian plates during the Eocene (about 40–45 myBP). See Grayum (1984) and the first half of this paper for further discussion.

Ariopsis. This monotypic Asian genus has been placed among colocasioid genera by all major authors of the Schottian and Englerian schools. Features of the genus most favoring such an association are peltate leaves, giant *Colocasia*-type hydathodes (otherwise known only from *Steudnera* and *Colocasia*), parietal placentation, and connate stamens. The last-mentioned feature is unique in Araceae, however, in that stamens of adjacent flowers are connate, in addition to those within each flower; thus, the stamens of *Ariopsis* are quite likely not homologous in this respect with those typical of Colocasioideae.

Character analysis suggests that *Ariopsis* is better transferred to subfamily Aroideae. It shares more advanced characters with the Englerian subtribe Arinae than with any other group: tuberous habit; reticulate venation (Ertl, 1932); secretion files; unilocular multiovulate ovaries with parietal placentation; orthotropous ovules; inaperturate, globose, spinose, trinucleate pollen; a base chromosome number of $x = 14$; and a unicellular chalazal endosperm chamber. That *Ariopsis* lacks the characteristic colocasioid venation is significant; that it lacks secretion tubes (French, 1988), the most important synapomorphy for the subfamily, is even more so. Moreover, ovular vasculature and morphology of *Ariopsis* are atypical for Colocasioideae (French, 1986c).

Ariopsis also has numerous features in common with *Arisaema* and *Pistia*. *Ariopsis* and *Pistia* share reticulate venation, basal fusion of spathe and spadix, a stipitate male portion of the spadix (unknown in Colocasioideae), multiovulate ovaries with parietal placentation, connate stamens with dehiscence by lateral pores (unique in Araceae to these two genera), orthotropous ovules, endospermous seeds, a base chromosome number of $x = 14$, and trinucleate pollen. The similarities in spadix structure between *Ariopsis* and *Pistia*/*Ambrosina* are so striking that *Ariopsis* is here treated as a sister taxon to the latter two genera.

Pinellia. In some respects the East Asian genus *Pinellia* is a typical member of subfamily Aroideae: it has a tuberous habit, ovate to compound leaves, reticulate venation, secretion files, a base chromosome number of $x = 13$, and inaperturate, globose, spinulose, starchy, trinucleate pollen. It is unusual, however, in sometimes having peltate leaves (P'ei, 1935), full fusion of the spathe with the female portion of the spadix, and unilocular uniovulate ovaries with basal placentation, hemianatropous ovules, and transverse anther dehiscence.

Largely because of the last-mentioned features, *Pinellia* shows greater overall phenetic resemblance to members of the Philodendroideae (*Typhonodorum*, *Peltandra*, *Callopsis*, Zomicarpeae) and Colocasioideae (*Hapaline*) than to any Aroideae. It agrees best with the latter genus, with which *Pinellia* shares a tuberous habit; basal fusion of the spathe and spadix; sterile male flowers (or naked regions) above and below the fertile male portion of the spadix; unilocular, uniovulate ovaries; more or less anatropous ovules; endospermous seeds; an identical base chromosome number ($x = 13$); and inaperturate, globose, spinose, starchy, trinucleate pollen.

In spite of the above evidence, *Pinellia* has here been conservatively maintained as a separate tribe in Aroideae. The genus lacks several important synapomorphies characterizing the Colocasioideae (including *Hapaline*): colocasioid venation, connate stamens, and secretion tubes. Those advanced characteristics shared with genera of other subfamilies are here interpreted as homoplasies. The geographic distribution of *Pinellia* tends to support its retention in Aroideae: it is the only aroid genus endemic to East Asia, a stronghold of this subfamily (*Typhonium*, of the Arinae, ranges into East Asia, *Arisaema* is highly diverse there, and *Amorphophallus* has an endemic section).

Thomsonieae. This pair of Old World genera was associated with the tribe Lasieae by Engler (1911), and with the Aroideae by most other authors. Character analysis strongly supports the latter view, which has been adopted in this paper (see detailed discussions under Lasieae and Arinae). The essence of the argument is that there is but a single important apomorphy shared by Thomsonieae with Lasieae that is not also shared with the Arinae, i.e., seeds lacking endosperm. The emphasis of this single character over the extensive list of putative synapomorphies linking the Arinae and Thomsonieae is indefensible.

The Thomsonieae also share certain features with *Ariopsis*, *Arisarum*, *Ambrosina*, and *Pistia*, though they do not appear closely related to any one of these. However, the occurrence in the last-named three genera of boat-shaped, striate pollen (uncommon in Araceae but basic to Thomsonieae) is viewed as significant, and the Thomsonieae have here been treated as the sister taxon to all four of these genera.

The distribution of Thomsonieae appears to be basically Laurasian. *Pseudodracontium* is exclusively South Asian. The vast and protean genus *Amorphophallus*, though extending throughout Africa (including Madagascar) and eastward to northeastern China, southern Japan, and Australia, likewise appears to be basically South Asian. The most primitive pollen type in the genus (striate) is almost restricted to the Asian species of the genus. The monotypic subgenus *Metandrium* (Stapf, 1923) and eight of the 11 sections of subg. *Amorphophallus* are endemic to or centered in continental South Asia (there are, however, two endemic African sections and one section restricted to East Asia, suggesting that the presence of *Amorphophallus* in these regions is of greater antiquity than that of, say, *Arisaema*, *Sauromatum*, or *Typhonium*).

Subfamily Aroideae is here interpreted to include Engler's subtribe Arinae (elevated to tribal rank) and tribe Thomsonieae, plus *Ariopsis*, *Arisaema*, *Pinellia*, *Arisarum*, *Ambrosina*, the Cryptocoryninae (here elevated to tribal rank), and *Pistia*. The sister group relationship of the subfamily as a whole is difficult to interpret. Although phenetically rather advanced overall, the Aroideae retain some primitive characteristics (e.g., microreticulate, perhaps starchless pollen; plurilocular ovaries with axile placentation; a base chromosome number of $x = 14$ or even $x = 7$; and distinct stamens). In some respects, it would be most parsimonious to pair the Aroideae with another "advanced" araceous subfamily, i.e., Philodendroideae or Colocasioideae; one might thereby minimize the number of separate derivations of laticifers, naked flowers, and monoecy. However, I have tentatively decided to align Aroideae with subfamily Lasioideae, mainly because of the prevalence of base chromosome numbers of $x = 13$ or 14 in both groups and the pronouncedly Laurasian distribution of the tribe Orontieae and all Aroideae.

Although the Lasioideae are in general much more primitive than Aroideae, laticifers, monoecy, and naked flowers are all known to occur in the former subfamily (laticifers in *Orontium* and throughout the Lasieae; monoecy in *Stylochaeton*; naked flowers in *Pycnospatha* of the Lasieae).

Cryptocoryninae. The two obviously related Southeast Asian genera *Cryptocoryne* and *Lagenandra* have been placed by all important authors of both the Englerian and Schottian schools among such genera as *Arisarum*, *Ambrosina*, *Pinellia* (all of Engler's Aroideae), and *Pistia*. This alignment has been based mainly on shared gynoecial characters: unilocular, pluriovulate ovaries with parietal or basal placentation; orthotropous ovules; and endospermous seeds. The character analysis performed in the present study showed a fair resem-

blance of Cryptocoryninae to these genera (mainly due to the gynoecial characters listed above), but even greater agreement with certain members of the Philodendroideae: the Aglaonemateae, *Peltandra* and *Typhonodorum*, but most strikingly with the Schismatoglottidinae.

Subtribe Schismatoglottidinae conforms in all respects to the gynoecial characteristics of the Cryptocoryninae. The two subtribes, which I previously (Grayum, 1984) included together in the same tribe, are both basically rhizomatous and show strong aquatic tendencies. Both at least occasionally have a stem endodermis, and they tend strongly toward conical, horned or tubular anther apices (unique in Araceae). The two have inaperturate, basically psilate, boat-shaped, starchy pollen, a type that is virtually unknown outside of Philodendroideae. Syncarpy, which is very rare in Araceae, occurs in both taxa (*Cryptocoryne* and *Piptospatha* sect. *Gamogyne*), and both have a Southeast Asian distribution.

The Cryptocoryninae are extremely well known cytologically but are difficult to comprehend. *Lagenandra* is clearly based on $x = 18$—a number typical of Philodendroideae but highly unusual in Aroideae. Most counts in *Cryptocoryne* are also typically philodendroid, i.e., $x = 17$, 18, and 21; however, many species are based on $x = 14$. *Cryptocoryne* is the only aroid genus to combine these fundamentally different base numbers.

French's (1988) startling revelation that Cryptocoryninae lack laticifers would appear to provide additional support for the original notion that the subtribe is most closely related to *Pistia*. It is, however, conceivable that laticifers have been convergently lost in these taxa, which share an aquatic lifestyle. But this argument cannot be made in the case of ovary vasculature, in which respect the Cryptocoryninae closely resemble *Pistia* and differ from all Philodendroideae (French, 1986c). Thus, the balance has recently tipped back in favor of an Aroideae alignment for the Cryptocoryninae. I herein elevate Cryptocoryninae to tribal rank, and return it to the subfamily Aroideae, near *Pistia*.

Arisarum, Ambrosina, Pistia. These three genera, which were analyzed separately, have been associated more or less closely with one another by most authors on aroid classification. *Arisarum* and *Ambrosina* have usually been included among elements here placed in subfamily Aroideae (e.g., by Schott, 1860; Hooker, 1883; Engler, 1920a; and Hutchinson, 1973). *Pistia* has variously been treated as a subtribe of the "tribe Arinae" (Hooker, 1883) or as a separate, monotypic tribe (Hutchinson, 1973) or subfamily (Engler, 1920a). Several authors, including Schott (1860), have excluded the genus from Araceae altogether. Lindley (1847) and Buscalioni & Lanza (1935) included *Ambrosina* together with *Pistia* in a separate family (Pistiaceae), to which Lindley also appended the genera composing the modern family Lemnaceae.

The notion that the Lemnaceae are related to or even derived from *Pistia* is by now quite firmly entrenched in the literature of botany (see, e.g., Takhtajan, 1980; Cronquist, 1981). *Pistia* is, however, a perfectly good (if superficially aberrant) aroid in all important details, whose closest relatives include the genera being considered along with it in this section. It appears to have nothing whatsoever to do with the Lemnaceae; that is, the Lemnaceae were not derived from *Pistia* nor, most likely, from anywhere near *Pistia*. The Lemnaceae may have a sister group relationship with the Araceae, which is about the closest conceivable connection they might have to *Pistia*, but even this is debatable. The two taxa have merely converged upon the floating, aquatic mode of existence and its attendant morphological adaptations. Full documentation for these statements is presented in Grayum (1984).

Character analysis indicates that *Arisarum*, *Ambrosina*, and *Pistia* are closely related to one another and somewhat more distantly to the rest of subfamily Aroideae. Basic characters of the group typical for Aroideae include a tuberous habit (except *Pistia*), reticulate venation (supposedly parallel in *Ambrosina*; Ertl, 1932), secretion files (except *Pistia*), advanced spathe and spadix types, unilocular, multiovulate ovaries with orthotropous ovules, distinct stamens (connate in *Pistia*), endospermous seeds, a base chromosome number of $x = 14$ ($x = 11$ in *Ambrosina*), a Mediterranean (Tethyan) distribution (except the cosmopolitan *Pistia*), and starchy pollen. They share with the Arinae characters of leaf morphology and gynoecial and ovular characters, although in their basically boat-shaped, striate-reticulate pollen they agree more with Thomsonieae. The troublesome absence of laticifers in *Pistia* (French, 1988) may be related to neoteny or reduction in this genus.

Pistia and *Ambrosina* appear more closely related to each other than either is to *Arisarum*. Both genera exhibit basal fusion of the spathe and spadix, a stipitate male portion of the spadix, reduction of the female portion to a single flower, apparently two stamens per male flower, and strikingly similar pollen exine sculpturing (see Grayum, in press a). They differ, however, in their growth habit, mode of anther dehiscence, base chromo-

some numbers ($x = 14$ in *Pistia*, $x = 11$ in *Ambrosina*), and pollen nuclear numbers (III in *Pistia*, II in *Ambrosina*). Thus, though these genera are here considered closely related, they are maintained in separate tribes.

Pistia and *Ambrosina* show more similarities to *Ariopsis* than to *Arisarum*. In fact, *Pistia* shares more putative apomorphies with *Ariopsis* than with *Ambrosina*. These mostly pertain to a strong overall resemblance in inflorescence structure, gynoecial morphology, stamens, ovules, and base chromosome number. *Ariopsis* differs from *Pistia*, *Ambrosina*, and the Cryptocoryninae in having globose, spinose, starchless pollen, and hence has been treated here as a sister group to both of those taxa rather than to *Pistia* alone.

Arisarum differs from *Pistia* and *Ambrosina* in several important respects: spathe free from the spadix, a nonstipitate male portion of the spadix, possession of a sterile apical appendage, a single stamen per male flower, several female flowers per inflorescence, and transverse anther dehiscence. The genus shows certain similarities to most of the other taxa in Aroideae (especially Thomsonieae, Arinae, and *Ariopsis*), but no compelling relationship to any one taxon. It is apparently quite isolated and is here maintained in its own tribe.

It should be clear from the foregoing discussion that, despite its peculiar aspect, *Pistia* is an integral part of the subfamily Aroideae. It clearly cannot be accorded separate subfamilial status since to do so would render the Aroideae paraphyletic.

Aroid Cladistics: A Beginning

A preliminary, quasi-cladistic model of the putative phylogenetic relationships of the important infrafamilial taxa in Araceae appears in Figure 1. This diagram was constructed in a piecemeal fashion, in a manner thought to best reflect the implications of the available data; it is not the product of a rigorous, computer-mediated algorithm. This subjective interpretation was necessary due to the small amount of characters employed in the analysis compared with the number of taxa under consideration. Computer analysis of aroid cladistics can be expected to provide valuable new insights, and work toward that goal is currently underway in at least two different laboratories. Meanwhile, highest priority should be given to the search for new kinds of systematically useful characters in Araceae, and to the expansion of the data base (for these and already established characters) to cover all genera of the family.

The fundamental dichotomy in Araceae (Fig. 1), as visualized as a result of the present investigations, pairs the Pothoideae and Philodendroideae, on one hand, against the Lasioideae and Aroideae, on the other. The former group consists of fundamentally rhizomatous or scandent plants with basically distichous leaves, a base chromosome number possibly other than $x = 7$ or 14 ($x = 12$?), and a largely Gondwanalandic distribution. The latter group consists of fundamentally rhizomatous or tuberous plants with basically spiral phyllotaxy, a base chromosome number of $x = 7$ or 14, and a basically Laurasian distribution. The position of Colocasioideae relative to these two groups remains unclear. Explanations for the two secondary dichotomies, Pothoideae/Philodendroideae and Lasioideae/Aroideae, are found under the headings "Homalomeninae, etc." and "Thomsonieae," respectively. Tertiary and lower-level dichotomies are discussed under the appropriate headings.

I consider the following aspects of Figure 1 to be particularly tentative: the position of Colocasioideae (which may even be diphyletic); the derivation of Zamioculcadeae, an isolated group of obscure affinity; the position of Spathicarpeae within Philodendroideae (this tribe may be more cladistically primitive than indicated); and the composition of the subfamily Lasioideae, the members of which are associated mainly on the basis of symplesiomorphies. The cladistic relationship among the various "alliances" of subfamily Philodendroideae is highly speculative, as is the composition of some of these groups (particularly the "*Aglaonema* alliance").

Aroid Classification: New and Old Perspectives

Inasmuch as aroid cladistics are still in the embryonic stage, the infrafamilial classification of Araceae is bound to remain in a state of flux. Thus, the classification at the end of this section (Table 5) is necessarily tentative, as are all other existing aroid classifications. Although there is a natural impatience on the part of workers in the field for a rigid and finalized system, our present comprehension of aroid phenetics falls far short of what will be needed for the construction of the finely resolved cladogram upon which such a classification must be based.

The linear order of the classification presented here reflects the constraints of the cladogram (Fig. 1); no additional significance should be imputed to the sequencing of taxa within larger groups. With the exception of Philodendroideae, no paraphyletic (according to the cladogram) groups have been accepted; otherwise, no attempt has been made to

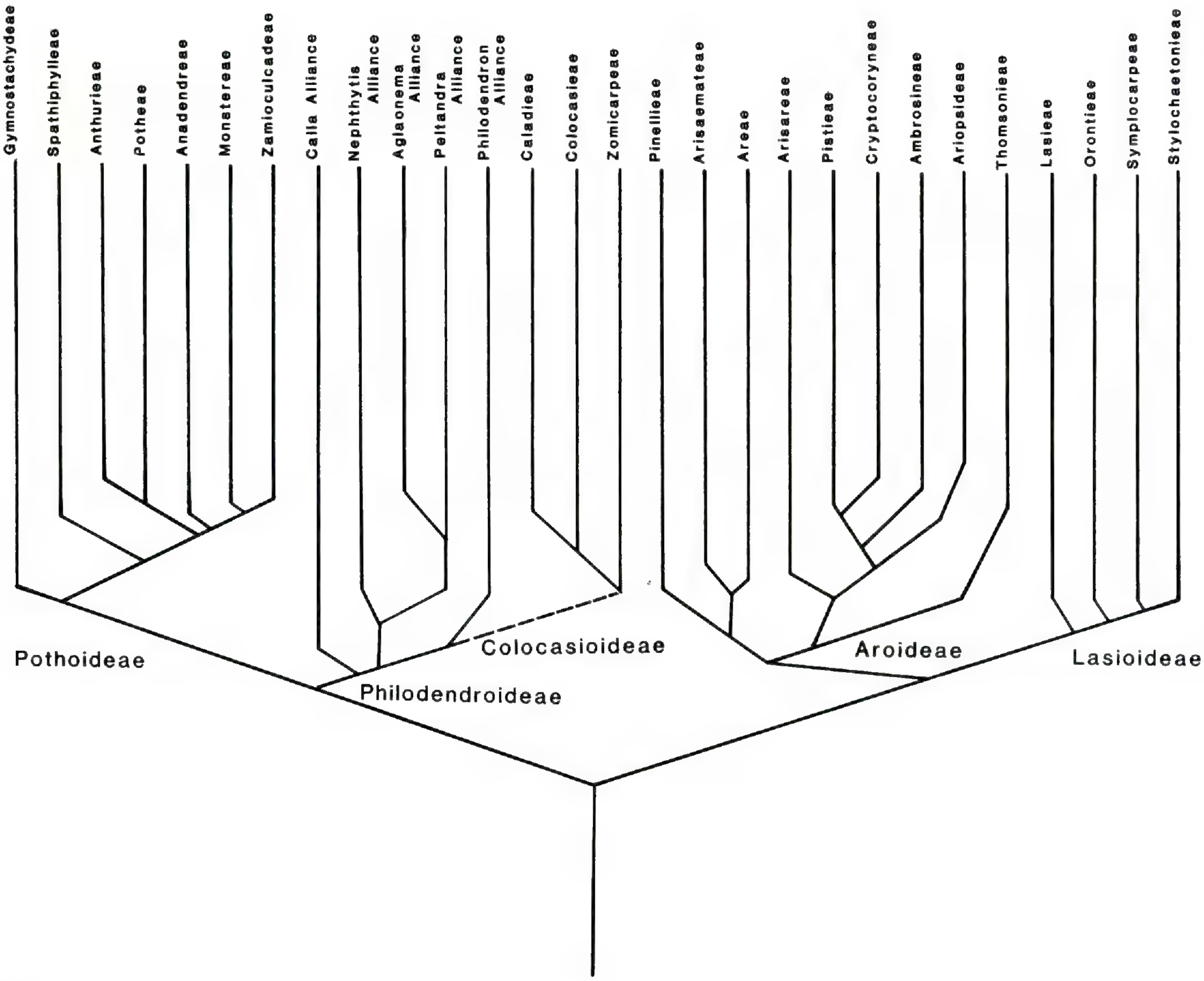

FIGURE 1. Proposed cladogram for major aroid subtaxa.

rigidly apply the criteria of cladistic classification. Since this classification is recognized as tentative, an effort was made to maintain nomenclatural stability by accepting Englerian ranks. In a few cases (particularly his tribes Colocasieae and Areae), however, this was deemed inadvisable. No systematic effort was made to ensure that various taxa at the same rank were equivalent in terms of their "level of peculiarity," and new suprageneric taxa have been described only where absolutely necessary.

The Araceae have here been grouped into five subfamilies in light of the information organized in the foregoing section. The system resulting from this arrangement most closely resembles that of Hotta (1970) in that *Acorus* has been removed from Pothoideae; Pothoideae and Monsteroideae are combined; and Calloideae are broken up (with *Calla* assigned to the Philodendroideae and the Orontieae to the Lasioideae, in both systems).

The present system differs from Hotta's mainly in that *Acorus* has now been removed from the Araceae altogether (Grayum, 1987), *Pistia* has been inserted directly into the Aroideae, and the Colocasioideae are here retained as a subfamily (rather than submerged in Philodendroideae, as Hotta has done). Hotta is probably at least partly correct on the latter issue, however: it is perhaps inevitable that at least part of the Colocasioideae will ultimately have to be subsumed in Philodendroideae. I tentatively maintain the former subfamily, owing to a good deal of uncertainty over the exact manner in which the two taxa are related, and particularly to some lingering suspicion that the Colocasioideae may in fact be diphyletic (see under Colocasioideae).

Significant departures from the Englerian system below the subfamily level are as follows (the rationales for all of these changes have been presented in previous sections): *Heteropsis* is moved from the Potheae into the Monstereae; the Monstereae are here envisioned as being more closely related to the Potheae than to the Spathiphylleae.

Culcasia is transferred out of Pothoideae into

TABLE 5. A preliminary new classification of the Araceae (with nomenclature based on Nicolson, 1984b).

Family Araceae Juss.

I. Subfamily Pothoideae Engl.
- 1. Tribe Gymnostachydeae Nakai (*Gymnostachys*)
- 2. Tribe Spathiphylleae Engl. (*Spathiphyllum*, *Holochlamys*)
- 3. Tribe Anthurieae Engl. (*Anthurium*)
- 4. Tribe Potheae Engl. (*Pothos*, *Pedicellarum*, *Pothoidium*)
- 5. Tribe Anadendreae Bogner & J. French (*Anadendrum*)
- 6. Tribe Monstereae Engl.
  - a. Subtribe Heteropsidinae Engl. (*Heteropsis*)
  - b. Subtribe Monsterinae Schott (*Rhaphidophora*, *Monstera*, *Amydrium*, *Epipremnum*, *Scindapsus*, *Alloschemone*, *Stenospermation*, *Rhodospatha*)
- 7. Tribe Zamioculcadeae Engl. (*Zamioculcas*, *Gonatopus*)

II. Subfamily Calloideae Schott
- A. *Calla* Alliance
  - 8. Tribe Calleae Schott (*Calla*)
- B. *Nephthytis* Alliance
  - 9. Tribe Nephthytideae Engl. (*Nephthytis*, *Anchomanes*, *Pseudohydrosme*)
  - 10. Tribe Callopsideae Engl. (*Callopsis*, *Ulearum*, *Filarum*, *Zomicarpella*)
  - 11. Tribe Montrichardieae Engl. (*Montrichardia*)
- C. *Aglaonema* Alliance
  - 12. Tribe Anubiadeae Engl. (*Anubias*)
  - 13. Tribe Zantedeschieae Engl. (*Zantedeschia*)
  - 14. Tribe Aglaonemateae Engl. (*Aglaonema*, *Aglaodorum*)
  - 15. Tribe Spathicarpeae Schott (*Mangonia*, *Asterostigma*, *Synandrospadix*, *Taccarum*, *Gorgonidium*, *Gearum*, *Spathantheum*, *Spathicarpa*)
  - 16. Tribe Dieffenbachieae Engl. (*Dieffenbachia*)
  - 17. Tribe Bognereae Mayo & Nicolson (*Bognera*)
- D. *Peltandra* Alliance
  - 18. Tribe Peltandreae Engl. (*Peltandra*, *Typhonodorum*)
  - 19. Tribe Arophyteae Bogner (*Arophyton*, *Carlephyton*, *Colletogyne*)
  - 20. Tribe Schismatoglottideae Nakai (*Schismatoglottis*, *Piptospatha*, *Bucephalandra*, *Phymatarum*, *Aridarum*, *Heteroaridarum*, *Hottarum*)
- E. *Philodendron* Alliance
  - 21. Tribe Culcasieae Engl. (*Culcasia*)
  - 22. Tribe Cercestideae Grayum[1] (*Cercestis*)
  - 23. Tribe Homalomeneae (Schott) M. Hotta (*Furtadoa*, *Homalomena*)
  - 24. Tribe Philodendreae Schott (*Philodendron*)

III. Subfamily Colocasioideae Engl.
- 25. Tribe Zomicarpeae Schott (*Zomicarpa*)
- 26. Tribe Colocasieae Engl.
  - a. Subtribe Protarinae (Engl.) Grayum[1] (*Protarum*)
  - b. Subtribe Steudnerinae Engl. & K. Krause (*Steudnera*)
  - c. Subtribe Remusatiinae Grayum[1] (*Remusatia*, *Gonatanthus*)
  - d. Subtribe Colocasiinae Schott (*Colocasia*, *Alocasia*)
- 27. Tribe Caladieae Schott
  - a. Subtribe Jasarinae Grayum[1] (*Jasarum*)
  - b. Subtribe Scaphispathinae Grayum[1] (*Scaphispatha*)
  - c. Subtribe Caladiinae Engl. & K. Krause (*Caladium*, *Xanthosoma*, *Chlorospatha*, *Aphyllarum*)
  - d. Subtribe Syngoniinae Schott (*Syngonium*)
  - e. Subtribe Hapalininae Engl. & K. Krause (*Hapaline*)

IV. Subfamily Lasioideae Engl.
- 28. Tribe Symplocarpeae Engl. (*Symplocarpus*, *Lysichiton*)
- 29. Tribe Orontieae R. Br. ex Dumort. (*Orontium*)
- 30. Tribe Lasieae Engl.
  - a. Subtribe Dracontiinae Schott (*Cyrtosperma*, *Lasia*, *Anaphyllum*, *Podolasia*, *Urospatha*, *Dracontioides*, *Dracontium*)
  - b. Subtribe Pycnospathinae Bogner (*Pycnospatha*)
- 31. Tribe Stylochaetoneae Schott (*Stylochaeton*)

TABLE 5. Continued.

V. Subfamily Aroideae Engl.
- 32. Tribe Thomsonieae Blume (*Pseudodracontium, Amorphophallus*)
- 33. Tribe Arisareae Dumort. (*Arisarum*)
- 34. Tribe Pinellieae Nakai (*Pinellia*)
- 35. Tribe Pistieae Blume (*Pistia*)
- 36. Tribe Cryptocoryneae Blume (*Cryptocoryne, Lagenandra*)
- 37. Tribe Ambrosineae Schott (*Ambrosina*)
- 38. Tribe Ariopsideae Engl. (*Ariopsis*)
- 39. Tribe Arisaemateae Nakai (*Arisaema*)
- 40. Tribe Areae Engl. (*Arum, Dracunculus, Helicodiceros, Theriophonum, Typhonium, Sauromatum, Eminium, Biarum*)

[1] Validation of new taxa and new combination:

Cercestideae Grayum, trib. nov. Philodendroidearum.

Plantae africanae praecipue scandentes canalibus laticiferis folia spiraliter disposita sine geniculo; antherae sine endothecio pollen amylaceum continentes; radices sine hypodermate sclerotico canalibus resiniferis; $x = 21$.

Protarinae, stat. nov.; Protareae Engl., in Engler & Prantl, Nat. Pflanzenfam. Nachtr. 3: 29, 34 (1906).

Remusatiinae Grayum, subtrib. nov. Colocasiearum.

Plantae orbis antiqui polline globoso spinoso trinucleato; spadix sine appendice sterili apicali.

Jasarinae Grayum, subtrib. nov. Caladiearum.

Plantae aquaticae submersae rhizomatosae venezuelensium caulibus sine systemate vasculari corticali foliis linearo-lanceolatis; ovarium uniloculare placentatione basali ovulis 2; semina sine endospermio; exinium pollinis omnino reticulatum; $x = 11$.

Scaphispathinae Grayum, subtrib. nov. Caladiearum.

Plantae brasiliensium sine floribus sterilibus ovariis unilocularibus placentatione basali; exinium pollinis verrucis applanatis multangulis.

the Philodendroideae in the neighborhood of *Philodendron*; *Cercestis* is removed from the Nephthytideae to its own tribe, Cercestideae, while the former tribe is enlarged to accommodate *Anchomanes* and *Pseudohydrosme* (formerly of the Thomsonieae); Cercestideae, Nephthytideae, and Montrichardieae are all transferred from Lasioideae to Philodendroideae; *Peltandra* and *Typhonodorum* are joined in a single tribe, the Peltandreae; the Callopsideae, Spathicarpeae, and Arophyteae are also moved from Aroideae to Philodendroideae. The Zomicarpeae are broken up, *Zomicarpa* being assigned to the Colocasioideae (as a separate tribe) and the remaining three genera to the Callopsideae (Philodendroideae). The last-mentioned subfamily, here much enlarged, has been divided into five informal "alliances."

The internal classification of subfamily Colocasioideae is changed to reflect a basic dichotomy, largely between New and Old World taxa. *Protarum* is transferred from the Aroideae into the Old World tribe Colocasieae as a separate subtribe; *Steudnera* is dissociated from *Remusatia* and *Gonatanthus* and is included in its own subtribe; the latter two genera (which probably ought to be combined) are placed in a new subtribe, Remusatiinae; *Jasarum* and *Scaphispatha* are each accorded separate subtribal status in the New World tribe Caladieae; *Syngonium* is included in this tribe as the monotypic subtribe Syngonieae. The Old World genus *Hapaline* agrees phenetically with the Caladieae and has been included there in its own subtribe.

The Lasioideae are expanded to include *Stylochaeton* (transferred from Aroideae) and the tribe Orontieae (sensu lato); the Thomsonieae, however, are moved out of Lasioideae and into Aroideae; *Ariopsis* is moved from the Colocasioideae into the Aroideae.

The following departures from Engler's usage (below the subfamily level) may be noted in the present system: nine tribes or subtribes (Potheae, Philodendreae, Nephthytideae, Colocasieae, Steudnerinae, Caladiinae, Orontieae, Thomsonieae, Zomicarpeae, and Areae) were judged to be more or less artificial, and variously disbanded; ten tribes or subtribes underwent a change of rank (Heteropsideae to Heteropsidinae; Schismatoglottidinae to Schismatoglottideae; Homalomeninae to Homalomeneae; Protareae to Protarinae; Syngonieae to Syngoniinae; Arisarinae to Arisareae; Atherurinae to Pinellieae; Arisaematinae to Arisaemateae; Ambrosininae to Ambrosineae; and Cryptocoryninae to Cryptocoryneae); subtribe Colocasiinae and tribe Callopsideae were enlarged; five tribes or subtribes (Acoreae, Typhonodoreae, Philodendrinae, Alo-

casiinae, and Arinae) were eliminated; and 10 (Gymnostachydeae, Anadendreae, Monsterinae, Cercestideae, Bognereae, Remusatiinae, Jasarinae, Scaphispathinae, Symplocarpeae, and Pistieae) were added on.

Many of the changes in the accompanying classification (Table 5) represent a return to pre-Englerian concepts. Although Engler's contributions revolutionized our understanding of aroid phenetics, I believe he made a fundamental and rather grave error in unduly emphasizing often superficial vegetative features (e.g., leaf venation and morphology) in constructing his classification. Engler's treatment of the tribes Lasieae and Thomsonieae provides a particularly glaring example of superficially convergent taxa juxtaposed on this basis; his inclusion of the genera *Anchomanes* and *Pseudohydrosme* within the Thomsonieae constitutes a somewhat less obvious case.

There are very good reasons why reproductive characteristics of higher plants should be accorded more taxonomic "weight" than vegetative features (see, e.g., Stebbins, 1970). Any mutation or recombination event significantly affecting the reproductive organs (e.g., a change in style length, petal color, timing of anther dehiscence or stigma receptivity, pollen exine ornamentation, chromosome features, etc.) would be much more likely to result in reproductive isolation, followed by speciation and a consequent cladistic dichotomy than would an event of similar magnitude affecting only vegetative organs. Therefore, within a given clade, one should expect to encounter considerably more variation in vegetative than in reproductive structures—as has long been intuitively appreciated by plant taxonomists. With regard to the Araceae, this would suggest that the strikingly similar leaf morphology of, say, *Dracontium* and *Amorphophallus* ought not to be emphasized so much as their radically different floral and pollen morphologies.

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APPENDIX 1. The aroid classification of Hutchinson (1973).

Tribe Acoreae	29%[1]
Acorus L.	
Gymnostachys R. Br.	
Tribe Orontieae	33%
Orontium L.	
Lysichiton Schott	
Tribe Spathiphylleae	25%
Spathiphyllum Schott	
Tribe Anthurieae	33%
Anthurium Schott	
Tribe Dracontieae	29%
Dracontium L.	
Echidnium Schott	
Dracontioides Engl.	
Symplocarpus Salisb. ex Nutt.	
Tribe Lasieae	30%
Urospatha Schott	
Lasia Lour.	
Podolasia N. E. Br.	
Holochlamys Engl.	
Cyrtosperma Griffith	
Anaphyllum Schott	
Tribe Potheae	23%
Pothos L.	
Pothoidium Schott	
Tribe Calleae	44%
Calla L.	
Pycnospatha Thorel ex Gagnepain	
Tribe Monstereae	58%
Stenospermation Schott	
Rhodospatha Poeppig	
Heteropsis Kunth	
Anadendrum Schott	
Amydrium Schott	
Epipremnum Schott	
Scindapsus Schott	
Rhaphidophora Hassk.	
Monstera Adans.	
Alloschemone Schott	
Tribe Stylochaetoneae	86%
Zamioculcas Schott	
Stylochaeton Lepr.	
Carlephyton Jum.	
Arophyton Jum.	
Colletogyne Buchet	
Tribe Richardieae	75%
Aglaonema Schott	
Aglaodorum Schott	
Montrichardia Crüger	
Zantedeschia Sprengel	
Anchomanes Schott	

APPENDIX 1. Continued.

Homalomena Schott	
Diandriella Engl.	
Plesmonium Schott	
Schismatoglottis Zoll. & Moritzi	
Aridarum Ridley	
Pseudohydrosme Engl.	
Bucephalandra Schott	
Piptospatha N. E. Br.	
Tribe Dieffenbachieae	79%
Dieffenbachia Schott	
Mangonia Schott	
Taccarum Brongn. ex Schott	
Synandrospadix Engl.	
Asterostigma Fischer & C. Meyer	
Gearum N. E. Br.	
Gorgonidium Schott	
Gonatopus Hook. f.	
Steudnera K. Koch	
Tribe Colocasieae	79%
Anubias Schott	
Remusatia Schott	
Colocasia Schott	
Gonatanthus Klotzsch	
Alocasia (Schott) Don	
Peltandra Raf.	
Callopsis Engl.	
Caladium Vent.	
Chlorospatha Engl.	
Xanthosoma Schott	
Aphyllarum S. Moore	
Typhonodorum Schott	
Ariopsis Nimmo	
Scaphispatha Brongn. ex Schott	
Hapaline Schott	
Tribe Philodendreae	75%

APPENDIX 1. Continued.

Culcasia P. Beauv.	
Cercestis Schott	
Rhektophyllum N. E. Br.	
Philodendron Schott	
Syngonium Schott	
Tribe Spathicarpeae	75%
Spathantheum Schott	
Spathicarpa Hook.	
Tribe Pistieae	86%
Pistia L.	
Tribe Pythonieae	84%
Zomicarpa Schott	
Amorphophallus Blume ex Decne.	
Thomsonia Wallich	
Pseudodracontium N. E. Br.	
Xenophya Schott	
Zomicarpella N. E. Br.	
Tribe Areae	81%
Arum L.	
Theriophonum Blume	
Helicodiceros Schott	
Protarum Engl.	
Dracunculus Miller	
Typhonium Schott	
Eminium (Blume) Schott	
Arisaema C. Martius	
Sauromatum Schott	
Biarum Schott	
Arisarum Miller	
Lagenandra Dalz.	
Cryptocoryne Fischer ex Wydler	
Pinellia Ten.	
Ambrosina Bassi	

[1] The numbers in this column refer to Howarth's (1957) "Advancement Indices."

THE PHYLOGENY AND CLASSIFICATION OF THE ZINGIBERALES[1]

W. John Kress[2]

Abstract

In the Zingiberales, a primarily tropical order of monocotyledons, most phylogenists currently recognize eight families: Musaceae, Strelitziaceae, Lowiaceae, Heliconiaceae, Zingiberaceae, Costaceae, Cannaceae, and Marantaceae. Some taxonomists still prefer the earlier classifications that included Strelitziaceae, Lowiaceae, and Heliconiaceae in Musaceae s.l., and Costaceae as a part of Zingiberaceae s.l. Attempts to reconstruct the phylogenetic history of the order have been made by Lane, Tomlinson, and Dahlgren & Rasmussen. An original analysis of the evolutionary relationships of the eight families of the Zingiberales based on the principles of phylogenetic systematics is presented here. The most parsimonious topology is (Musaceae (Strelitziaceae (Lowiaceae (Heliconiaceae ((Zingiberaceae, Costaceae) (Cannaceae, Marantaceae)). The cladogram rejects the recognition of Musaceae s.l. as an evolutionary group. A new phylogenetic classification based on the cladogram is proposed that recognizes eight families, two superfamilies, and five suborders within the Zingiberales.

"The Scitamineae [Zingiberales] is a very natural order of monocotyledons, somewhat comparable in its homogeneity to grasses, palms or orchids. . . , long recognized by taxonomists as a natural entity" (Tomlinson, 1962).

"The Order Zingiberales is well characterized and sharply defined; its limits have occasioned no controversy . . . . One could wish that the families in all orders were as well marked and sharply defined as those in the Zingiberales" (Cronquist, 1981).

"The Zingiberiflorae, whether treated as a separate superorder, as here, or an order in a more widely circumscribed unit, is one of the most indisputably natural suprafamilial groups" (Dahlgren, Clifford & Yeo, 1985).

The Zingiberales, or Scitamineae, are a group of monocotyledons whose members are almost entirely restricted to tropical regions. As indicated by the above quotations, the order is widely accepted by most taxonomists and phylogenists to be a distinctly circumscribed "natural" or monophyletic lineage of plants. No morphological characters are in conflict with the acceptance of the Zingiberales as a monophyletic group.

In a brief diagnosis of the morphological and anatomical characters that distinguish the order, Tomlinson (1962) included the following: rhizomatous herbs; leaves with open, sometimes ligulate sheaths; lamina entire with lateral veins diverging from a common midrib, one-half of blade completely rolled around the other during development; hairs commonly unicellular; guard cells each with two narrow lateral subsidiary cells parallel to the pore; hypodermis of colorless cells below each surface of lamina; air canals in leaf axis segmented by transverse diaphragms containing stellate cells; leaf axis with a single main arc of large vascular bundles and subsidiary systems of smaller bundles; silica cells or stegmata associated with vascular bundles in all parts except roots; inflorescence terminal or lateral, commonly racemose with conspicuous bracts; flowers (Fig. 1) zygomorphic, perianth consisting of separate calyx and corolla; fertile stamens usually five or one; one to five stamens usually represented by staminodes; ovary inferior, three-locular, with one to many ovules in each locule; seeds with abundant endosperm, often arillate.

In reviewing these characters and subsequently studied features, Dahlgren and coworkers (1985) listed six apomorphies for the Zingiberales (their

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Professor P. Barry Tomlinson's enthusiasm for large monocots provided the original inspiration for my studies of the Zingiberales. I dedicate this paper to him.

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Superorder Zingiberiflorae): root hair cells shorter than other epidermal cells, sieve tube plastids containing starch, presence of silica bodies, epigynous flowers, lack of distinctive apertures on the pollen grains, and the occurrence of arillate seeds. Although some of the features vary within families, these uniquely derived states distinguish the Superorder Zingiberiflorae from its closest relatives in the monocotyledons. However, for most botanists it is the herbaceous arborescent stem, the distichous phyllotaxy, the large petiolate leaves with blades possessing transverse venation, the conspicuous, colorful bracteate inflorescences, and the substitution of one to five staminodia for the fertile stamens that distinguish the Zingiberales as a homogeneous and natural group.

The distinctiveness of the Zingiberales has caused controversy in determining the relationship of the order to other monocotyledons. Based on similarity in inflorescence and flower structure (primarily the large, conspicuous bracts and petaloid perianths) most modern phylogenists have agreed that the Zingiberales and Bromeliales (containing the single family Bromeliaceae) have shared a most recent common ancestor (Hutchinson, 1973; Stebbins, 1974; Takhtajan, 1980; Cronquist, 1978, 1981; but see Thorne, 1976, and Walker, unpublished). Although the homologies of the inflorescence bracts and perianths are not unequivocal, several possibly unique chemical characters (myricetin and/or quercitin glycosides) shared by the two orders also suggest a common ancestor (Williams & Harborne, 1977). Based on the presence of the conspicuous petaloid perianth, Dahlgren et al. (1985) have hypothesized the Zingiberales as the sister group to their larger taxon Bromeliiflorae, which includes the Bromeliaceae, Velloziaceae, Philydraceae, Haemodoraceae, Pontederiaceae, Sparganiaceae, and Typhaceae. Until contrary evidence becomes available, the Bromeliales serve as the best outgroup to the Zingiberales in the monocotyledons.

The common ancestor of the Zingiberales–Bromeliales lineage (Zingiberidae of Cronquist) and other monocots is even more unclear. The presence of two distinctive perianth whorls of sepals and petals that may coalesce but never fuse and the presence of starchy endosperm are shared with a Commelinalian ancestor (Hutchinson, 1973). The septal nectaries, vessels primarily in the roots, and several chemical characters (e.g., chelidonic acid) ally the Zingiberales to the Lilialian lineage (Takhtajan, 1980). Dahlgren et al. (1985) have shown that starchy endosperm, epicuticular wax of the *Strelitzia* type, UV-fluorescent organic acids in the cell walls, and two or four subsidiary cells in the stomatal complex are apomorphies of the Zingiberiflorae–Bromeliiflorae–Commeliniflorae lineage. These last characters provide the best evidence for accepting a common ancestry with a Commelinalian line. However, Walker (1987) has chosen to derive his Zingiberidae (excluding the Bromeliales), and its sister group, the Pontederiidae (Haemodoraceae, Pontederiaceae, and Philydraceae), directly from a primitive Liliid lineage.

History of the Classification of the Zingiberales

The history of the classification of the Zingiberales, like many tropical plant groups, is one of continual refinement and division (Table 1). Bentham & Hooker (1883) recognized four tribes in their Ordo (Family) Scitamineae: Zingibereae, Maranteae, Canneae, and Museae. These tribes were delineated by the degree of fusion of the perianth parts, the number of fertile stamens and staminodes, the number of locules per anther, the style and stigma type, the number of ovules per locule, and the shape of the embryo (Fig. 1). Petersen (in Engler & Prantl, 1889) raised the rank of the four tribes to family and subdivided the Musaceae, which was held together primarily by the number of fertile anthers, into the tribes Museae (containing *Musa*, *Ravenala*, and *Strelitzia*) and Heliconieae (*Heliconia*). The solitary ovule per locule, septicidal fruit dehiscence, and inverted symmetry of the flowers distinguished *Heliconia* from the other members of the Musaceae. *Orchidantha*, the sole genus in the Lowiaceae, was excluded from the Scitamineae of Bentham & Hooker, but recognized as a possible member of the group by Petersen.

Schumann in *Das Pflanzenreich* (in Engler, 1900, 1902, 1904) further subdivided the Order Scitamineae by segregating genera into subfamilies. In the Zingiberaceae, the Costoideae was recognized as distinct from the Zingiberoideae on the basis of the spiral phyllotaxy and lack of essential oils in the former. The Musoideae (*Musa*), Strelitzioideae (*Strelitzia*, *Ravenala*, and *Heliconia*), and the Lowioideae (*Orchidantha*) were given subfamilial rank in the Musaceae. Here, *Heliconia*, *Strelitzia*, and *Ravenala*, possessing distichous phyllotaxy and hermaphroditic flowers, were separated from *Musa*, which possesses spirally arranged vegetative parts and unisexual flowers. Further subdivision separated the Strelitzioideae into the Strelitzieae (*Strelitzia* and *Ravenala*), with multiovulate locules and arillate seeds, from the Heliconieae (*Heliconia*), with uniovulate locules and no arils.

TABLE 1. Systems of classification of the Zingiberales.[1]

Bentham & Hooker (1883)	Petersen (Engler & Prantl, 1889)	Schumann (Engler, 1900, 1902, 1904) Winkler; Loesener (Engler & Prantl, 1930)
Family: Scitamineae	No rank	Order: Scitamineae
Tribes	Families	Families
Museae (*Musa, Ravenala, Strelitzia, Heliconia*)	Musaceae Tribes Museae (*Musa, Ravenala, Strelitzia*)	Musaceae Subfamilies Musoideae (*Musa*) Strelitzioideae Tribes Strelitzieae (*Strelitzia, Ravenala*) Heliconieae (*Heliconia*)
	Heliconieae (*Heliconia*)	Lowioideae
Zingibereae	Zingiberaceae	Zingiberaceae Subfamilies Zingiberoideae
		Costoideae
Maranteae	Marantaceae	Marantaceae
Canneae	Cannaceae	Cannaceae

Hutchinson (1934, 1959, 1973), who used the ordinal name Zingiberales (after Nakai, 1941), accepted the divisions of Schumann, but raised to the rank of family the Strelitziaceae (including *Heliconia*) and Lowiaceae. He also further subdivided the Zingiberaceae into four tribes of equal status.

In most modern taxonomic treatments of the Zingiberales, eight families are recognized: Zingiberaceae, Costaceae, Marantaceae, Cannaceae, Musaceae, Strelitziaceae, Heliconiaceae, and Lowiaceae (Table 1). Nakai (1941) first suggested that the Costoideae and the Heliconieae be raised to family rank. The nonaromatic vegetative body, spirally arranged leaves, and anther appendages were cited by Nakai as separating the Costaceae from the Zingiberaceae. The uniovulate locules, exarillate seeds, and capitate stigmas of the Heliconiaceae distinguished that taxon from the other families of the order. Subsequently Tomlinson (1962, 1969), in his investigations of the anatomy of the order, pointed out that the degree of morphological and anatomical differences among the eight entities is about the same (see also above quote by Cronquist), and therefore accepted the classification of Nakai. Stebbins (1974), Takhtajan (1980), Cronquist (1978, 1981), and Dahlgren and

TABLE 1. Continued.

Hutchinson (1934, 1959)	Nakai (1941); Tomlinson (1962); Takhtajan (1980); Cronquist (1981); Dahlgren et al. (1985)	Kress[2]
Order: Scitamineae (later Zingiberales)	Order: Zingiberales	Order: Zingiberales
		Suborders
		Musineae
Families	Families	Family
Musaceae (*Musa*)	Musaceae (*Musa, Ensete*)	Musaceae (*Musa, Ensete*)
		Strelitzineae
		Family
Strelitziaceae (*Strelitzia, Ravenala, Phenakospermum, Heliconia*)	Strelitziaceae (*Strelitzia, Ravenala, Phenakospermum*)	Strelitziaceae (*Strelitzia, Ravenala, Phenakospermum*)
		Lowineae
		Family
Lowiaceae	Lowiaceae	Lowiaceae
		Heliconineae
		Family
	Heliconiaceae (*Heliconia*)	Heliconiaceae (*Heliconia*)
		Zingiberineae
		Superfamilies
		Zingiberareae
		Families
Zingiberaceae		
Tribes		
Zingibereae	Zingiberaceae	Zingiberaceae
Hedychieae		
Globbeae		
Costeae	Costaceae	Costaceae
		Cannariae
		Families
Marantaceae	Marantaceae	Marantaceae
Cannaceae	Cannaceae	Cannaceae

[1] After Tomlinson (1962) and Kress (1984).
[2] See Table 5.

coworkers (1983, 1985) have followed Nakai and Tomlinson in the recognition of eight families in the order.

The changes in family concepts within the Zingiberales during the last hundred years can be attributed in part to an increased understanding over time of character distribution within the taxa. In the early classifications of the 1800s comparatively little was known about the number of taxa and the amount of character variation within each group. Hence, similarities among the taxa were stressed in devising classifications, as it was easier to fit new taxa into fewer categories. As more genera and species were discovered and described, discontinuities in character variation became more obvious and differences separating taxa became more apparent. The current recognition of eight families within the order is a direct result of the much larger data base of taxa and character distribution available today. An even further division of families may occur as additional data become available.

Phylogenists who have studied the Zingiberales have been mostly concerned with the degree of

character differences between families. The question of the monophyly of the taxa themselves has not been adequately addressed, i.e., the families have been defined in terms of grades and not clades. For example, if the Strelitziaceae of Hutchinson (including Heliconiaceae; 1934, 1959) or Loesener's Zingiberaceae (including Costaceae; in Engler & Prantl, 1930) are not monophyletic groups, then support is provided for the recognition of equal taxonomic status for the included families. However, if these larger taxonomic groups are descendents of a unique common ancestor (monophyletic), then the taxonomic status of each group becomes more of a practical matter than a phylogenetic one.

In this paper, the eight families of Nakai and Tomlinson are accepted as working hypotheses of monophyletic groups within the Zingiberales. Evidence from the cladistic analyses of the order (provided below) is used to test hypotheses on family boundaries.

The Families of the Zingiberales

Detailed descriptions of each of the eight families of the Zingiberales have been provided in several recent publications (Tomlinson, 1969; Cronquist, 1981; Dahlgren et al., 1985) and will not be repeated here. Those family characteristics pertinent to this discussion, including autapomorphies, are given below (also see Fig. 1).

Family Musaceae A. L. Jussieu (1789)

The two genera of the Musaceae, *Musa* (35 species) and *Ensete* (seven species), are restricted to the Paleotropics of Africa, eastern Asia, Australia, and the South Pacific. The lacticifers, specialized laminal mesophyll with vasculated and nonvasculated parenchymatous septa, spirally arranged phyllotaxy, unisexual flowers, and baccate fruits distinguish the members of the Musaceae from other Zingiberales.

The commercial importance of bananas has always focused attention on this family, especially the parthenocarpic hybrid triploids. *Ensete*, formerly included within *Musa*, differs in its monocarpic habit, the presence of warty exinous protuberances on the pollen grain surface, the large seeds, and the "T-shaped" embryo.

Family Strelitziaceae Hutchinson (1934)

The three genera and seven species of the family, *Strelitzia* (five species), *Ravenala* (one species), and *Phenakospermum* (one species), are restricted to southern Africa, Madagascar, and South America, respectively. Nakai (1941) erected a new genus *Musidendron*, not recognized by most taxonomists, for the members of *Phenakospermum* possessing a ligneous trunk, sessile inflorescence, differently colored bracts and flowers, and 8–12 rows of ovules per locule. Information on the geographic variation of *Phenakospermum* is insufficient at this time to evaluate adequately the validity of this segregate genus (Kress, unpublished). Unique features of the Strelitziaceae are the woody trunk (lost in some members of *Strelitzia*), the three free sepals, the two fused petals that enclose the five (or six in *Ravenala*) fertile stamens (Fig. 1), and the woody, loculicidal capsular fruit.

The close relationship of these three genera has been accepted by most authors (but see Lane, 1955). Early taxonomists included the Strelitziaceae in a broadly circumscribed Musaceae but often recognized it at some subfamilial ranking. On the basis of the distichous phyllotaxy and hermaphroditic flowers, Hutchinson (1934, 1973), deemphasizing the specialized features that set the genus apart, included *Heliconia* in his Strelitziaceae.

Family Lowiaceae Ridley (1924)

The single genus of the family, *Orchidantha*, with five to eight species, is found in Southeast Asia and some Pacific islands. The specialized leaf blade with mesophyll of irregularly arranged large and small cells (Tomlinson, 1962), several pairs of longitudinal veins parallel to the distinct midrib (Lane, 1955; Hutchinson, 1973), and the elaboration of the adaxial petal into a large labellum are among the obvious autapomorphies of the family.

Orchidantha has always been considered an unusual member of the Zingiberales and is most commonly classified either as a subfamily of or a separate family allied to the Musaceae. Lane (1955) accepted the Lowiaceae and stated that they are "probably as close to the Marantaceae or Zingiberaceae as to the Musaceae." No other phylogenists have accepted Lane's ambiguous placement of the family. The Lowiaceae are among the most poorly known taxa in the order in terms of taxonomy, general morphology, embryology, chemistry, and ecology.

Family Heliconiaceae Nakai (1941)

The single genus *Heliconia* has perhaps 250 species that are distributed primarily in the Neotropics. Six species (at one time segregated as the genus *Heliconiopsis* Miquel) are found in the South Pacific from Samoa westward to Indonesia (Kress, 1990). The inverted symmetry of the flowers (the median sepal is adaxial in *Heliconia*), the presence of a single staminode opposite the un-

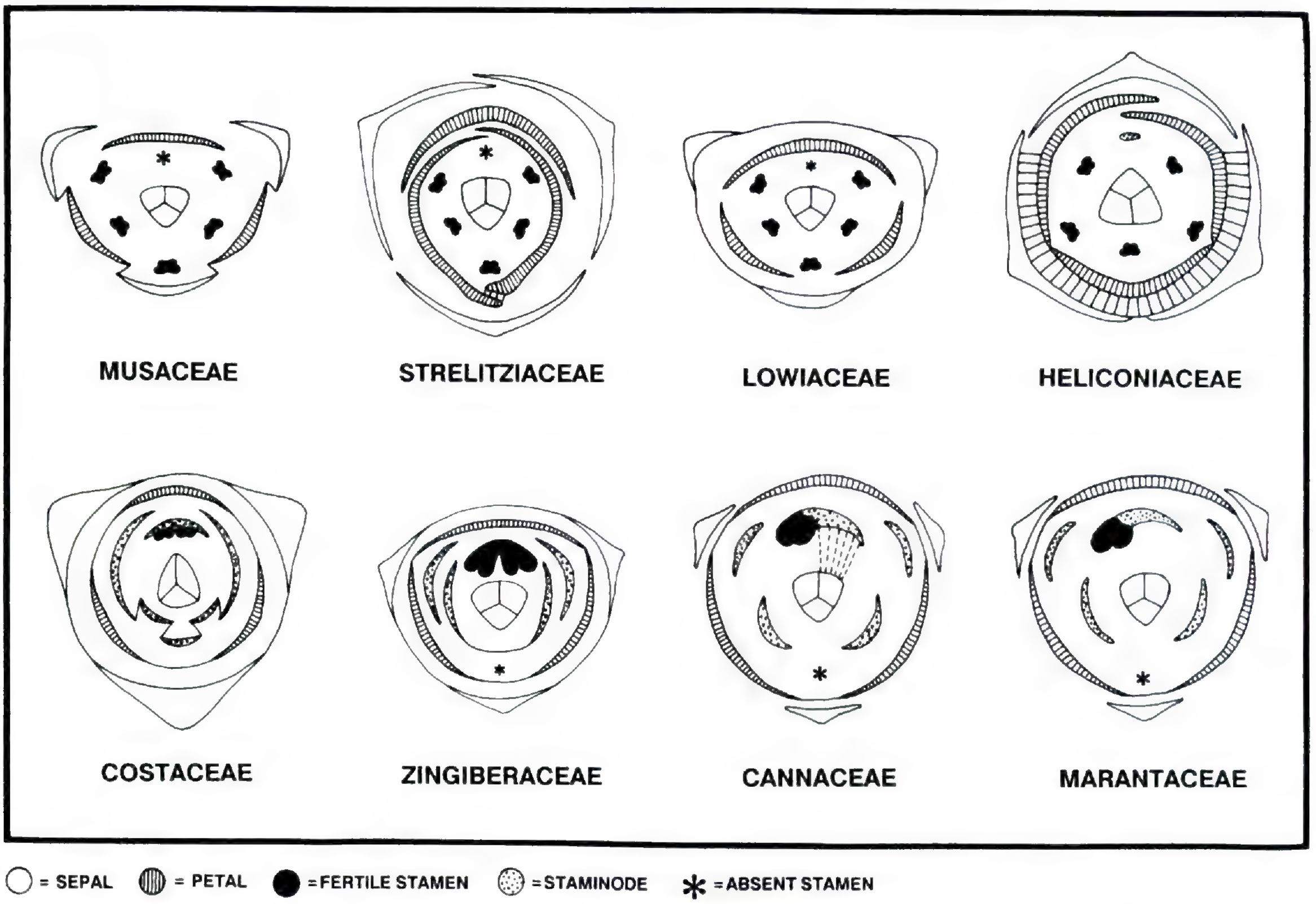

FIGURE 1. Floral diagrams of the eight families of the Zingiberales. For variable characters (e.g., stamen and staminode number) the most common state of the family is indicated. (Not drawn to scale; based on Lane (1955), Maas (1972), Kirchoff (1983a), and Kress (unpublished).)

paired sepal (Fig. 1), the heteropolar pollen grains, a single ovule per locule, and the drupelike fruits are autapomorphies of the family.

Heliconia has been variously associated with the Musaceae and the Strelitziaceae, depending upon the importance placed on the distichous phyllotaxy and hermaphroditic flowers (then placed with the Strelitziaceae) versus the terminal inflorescence, partial fusion of the calyx and corolla, and exarillate seeds (then placed with the Musaceae). Currently most taxonomists accept Nakai's placement of the genus in its own family Heliconiaceae.

FAMILY ZINGIBERACEAE LINDLEY (1835)

The Zingiberaceae, the largest family in the Zingiberales, consist of approximately 50 genera and 1,000 species. Their distribution is pantropical but concentrated in the Old World, especially in Southeast Asia. Because of the ephemeral flowers, taxonomic study of the family is difficult and a classification is still incomplete. The family has been variously divided into a number of tribes. Burtt & Smith (1972) recognized four tribes: Hedychieae, Zingibereae, Alpinieae, and Globbeae. The fusion of the lateral staminodes of the inner staminal whorl into a labellum (Fig. 1), the presence of two epigynous nectariferous glands at the base of the style, and the occurrence of cells containing essential or ethereal oils are autapomorphies of the family. Other floral characters normally associated with the Zingiberaceae, such as the presence of a single fertile tetrasporangiate anther and the slender style, which lies between the two pollen sacs, are derived characters shared with the Costaceae, hence are not apomorphic in the family.

The Zingiberaceae have always been considered a natural group within the Zingiberales, with or without the Costaceae (see below). The reduction of the number of fertile pollen-bearing stamens to one, and the modification of the other stamens into petaloid staminodes, is a characteristic "trend" in the order and is carried to an extreme in the Marantaceae and Cannaceae.

FAMILY COSTACEAE NAKAI (1941)

The Costaceae, consisting of four genera and about 150 species, are distributed pantropically. The largest genus, *Costus* (100 species), is most

diverse in the Neotropics and is also found in Africa, Asia, and northern Australia. *Monocostus* (one species) and *Dimerocostus* (two species) are restricted to the New World tropics. *Tapeinochilos* (20 species), the most poorly understood genus in the family, extends through New Guinea, Indonesia, and tropical Australia. The well-developed (sometimes branched) aerial stem, distinctive staircaselike spirally arranged phyllotaxy, fusion of the five staminodes into a labellum (Fig. 1), petaloid filament and connective, and distinctly aperturate acetolysis-resistant pollen grain wall are characters unique to the Costaceae. The multicellular trichomes and the poorly developed system of air canals in the leaf axis (Tomlinson, 1962) may also be autapomorphies.

The Costaceae were at first always classified as a subdivision of the Zingiberaceae, either as a subfamily or tribe. Nakai's (1941) suggestion that the Costaceae deserved familial rank was supported by Tomlinson's (1962) anatomical investigations and has been accepted by many recent phylogenists. Early taxonomists united the two families on the basis of several inflorescence and floral characters (see above under Zingiberaceae), which as Tomlinson (1962) pointed out, "may indicate evolution from a common ancestor, yet total differences between them warrant independent familial rank."

FAMILY CANNACEAE A. L. JUSSIEU (1789)

Canna, the solitary genus in the family, is primarily found in the New World tropics and subtropics. The pantropical distribution of *C. indica* is most likely the result of human dispersal. Estimates on the number of species in *Canna* range from 9 to 50 (Segeren & Maas, 1971; Maas, unpublished). The presence of mucilage cells and a petaloid style fused to the single fertile stamen (Fig. 1) are the most obvious autapomorphies of the family. Many other features that readily distinguish the Cannaceae from the other families of the order, such as the asymmetric flowers, reduction of fertile anthers to a single bisporangiate anther sac, and secondary pollen presentation, are shared with the Marantaceae.

The Cannaceae have been recognized by all taxonomists as a distinct taxonomic entity, usually at the family level within the Zingiberales. The morphological similarities with the Marantaceae have invariably led to the close placement of the Cannaceae with that family in all classifications proposed.

FAMILY MARANTACEAE PETERSEN IN ENGLER & PRANTL (1889)

The Marantaceae are the second-largest family in the order, with 30 genera and 450–500 species. Although the geographic distribution is pantropical, three-quarters of the species, many in the large genus *Calathea*, are found in the Neotropics. The classification of the family is still inadequately resolved with no general consensus on subfamilial divisions (Andersson, 1981; H. Kennedy, pers. comm.). Apomorphies of the family include the leaf pulvinus, sigmoid lateral veins and evenly spaced cross-veins of the leaf blade, terminal enantiomorphic pairs of flowers, two inner staminodes (cucullate and callous staminodes, which are modified into structures for the explosive release of the pollen at pollination), and the single ovule per locule.

As with the Cannaceae, all phylogenists have agreed upon the separate familial status of the Marantaceae. Based on the highly modified zygomorphic flowers and the reduction in the number of fertile pollen-bearing stamens to a single bisporangiate pollen sac, most taxonomists consider the Marantaceae to be the most derived family of the Zingiberales.

Past Phylogenetic Investigations of the Zingiberales

FOSSIL EVIDENCE

In some cases fossils may provide information on the evolutionary history of a plant group. For the Zingiberales, fossil records have been attributed to five of the eight families. Most of the fossil specimens have been collected in Eocene deposits. Eocene fruits of the fossil taxa *Musa cardiosperma* have been found in India (Jain, 1963; Daghlian, 1981). Various vegetative structures found in the same Deccan Intertrappean beds of India have been tentatively assigned to the Heliconiaceae (Trivedi & Verma, 1971). Leaf specimens of the genus *Musophyllum* found in neotropical Tertiary beds also have been attributed to *Heliconia* (Berry, 1921; Simmonds, 1962). The oldest fossils of the order are leaves of the Zingiberaceae in the fossil genus *Zingiberopsis* from the late Cretaceous (Hickey & Peterson, 1978). Ginger fruits and arillate seeds of the fossil *Spirematospermum* are well represented in Eocene through Miocene sediments of Denmark (Friedrich & Koch, 1970, 1972; Koch & Friedrich, 1971). Fossil leaves from the Eocene of Texas attributable to a possibly extinct genus of the Cannaceae have been reported by Daghlian

(1982). Eocene deposits from England have yielded fossils resembling the leaves of the Marantaceae (Cronquist, 1981). Wodehouse (1932) suggested that fossil pollen of the Musaceae and Cannaceae occur in the Eocene Green River Flora of the western United States. However, the fragile, acetolysis-susceptible nature of the pollen wall of the Zingiberales, which would not stand up to normal processes of fertilization, makes this report suspect. No fossil records of the Strelitziaceae, Lowiaceae, or Costaceae have been reported.

The reports of fossil remains of the Zingiberales do not shed much light on the historical relationships of the families. Recognizable "gingers" appeared by the late Cretaceous and most of the families apparently had differentiated by the early Tertiary. The distinctive venation of the leaves of the Zingiberales has been important in allowing fossil taxa to be assigned to particular families (Hickey & Peterson, 1978). However, the lack of fossil flowers has prevented any paleontological interpretations of the evolution of the reproductive structures in the order.

PREVIOUS PHYLOGENETIC ANALYSES

Most classifications of the Zingiberales (Table 1) can be interpreted as a statement on the evolutionary relationships of the taxa. For example, the close relationship, at least morphologically, of the Cannaceae and Marantaceae was implied by the association of these two families in all classifications. The broad interpretation of the Musaceae (sometimes excluding *Orchidantha*) to include all genera with five or six stamens likewise was a statement on the evolutionary "closeness" of those taxa. The same is true of the consistent classification of the Zingiberaceae–Costaceae complex. However, explicit statements on the actual phylogenetic history of the order are few, especially in terms of sister-group relationships.

The first diagrammatic representation of the relationships of the groups within the Scitamineae (Fig. 2) was applied in the frontispiece of a book on bananas by Reynolds (1927). Although Reynolds did not explain or justify his illustration, the morphological similarities and perhaps evolutionary associations among the taxa of the closest relatives of *Musa* are depicted: similar taxa share a common branch or "sympodium" of the vegetative axis, thereby representing the genealogical history of the order.

Lane's analysis. Lane (1955), the first to consider in detail the relationships within the Zingiberales, was most concerned with the taxa of the Musaceae s.l. Based on the reduced ovule number, flower orientation, and anatomical structure of the root, he believed the genus *Heliconia* to be the most derived member of the family. The similarities to *Musa* (terminal inflorescence, lack of aril, baccate fruit, and similar vegetative habit) led him to state that these two families "have been derived together, from a stock early divergent from the rest of the family . . . ." He also believed that *Strelitzia* and *Phenakospermum* are more closely related to each other than either is to *Ravenala*, which he considered the least derived genus of the family. Lane provided a classification of the Musaceae that included two subfamilies and three tribes based on these relationships. The subfamily Musoideae was made up of the tribe Ravenaleae (*Ravenala*), tribe Strelitzieae (*Strelitzia* and *Phenakospermum*), and tribe Museae (*Musa* and *Ensete*). The second subfamily, Heliconioideae, contained only the genus *Heliconia*. In a cladistic sense Lane's classification is difficult to reconcile with his statements on relationships, i.e., *Heliconia*, which he stated has shared a unique common ancestor with *Musa*, was placed in a separate subfamily. Obviously Lane accepted the phenetic view that the degree of character differences, not the cladistic patterns, should determine the hierarchical level of classification.

Lane briefly mentioned that the cymose-type inflorescences of the other families of the Scitamineae indicate that they were not closely related to the Musaceae. The position of *Orchidantha* in the order was also unclear to him. Lane's brief treatment, although somewhat unusual in light of our current knowledge of the taxa, was the first to address concisely the evolutionary relationships of the genera of the Musaceae s.l. in terms of ancestors and descendants.

Tomlinson's analysis. The exhaustive investigations of the anatomy of the Zingiberales by Tomlinson in the 1950s and 1960s served as the impetus for his pivotal paper on the phylogeny of the order (Tomlinson, 1962). Building on the work of earlier taxonomists, Tomlinson combined both morphological and anatomical characters into an analysis of the evolutionary relationships of the eight families he recognized in the Scitamineae (Table 1). Based on the structure of the guard cells, presence or absence of raphide sacs, and structure of the root stele, he suggested that the eight families could be separated into four "natural groups . . . according to greatest degree of affinity": Group 1

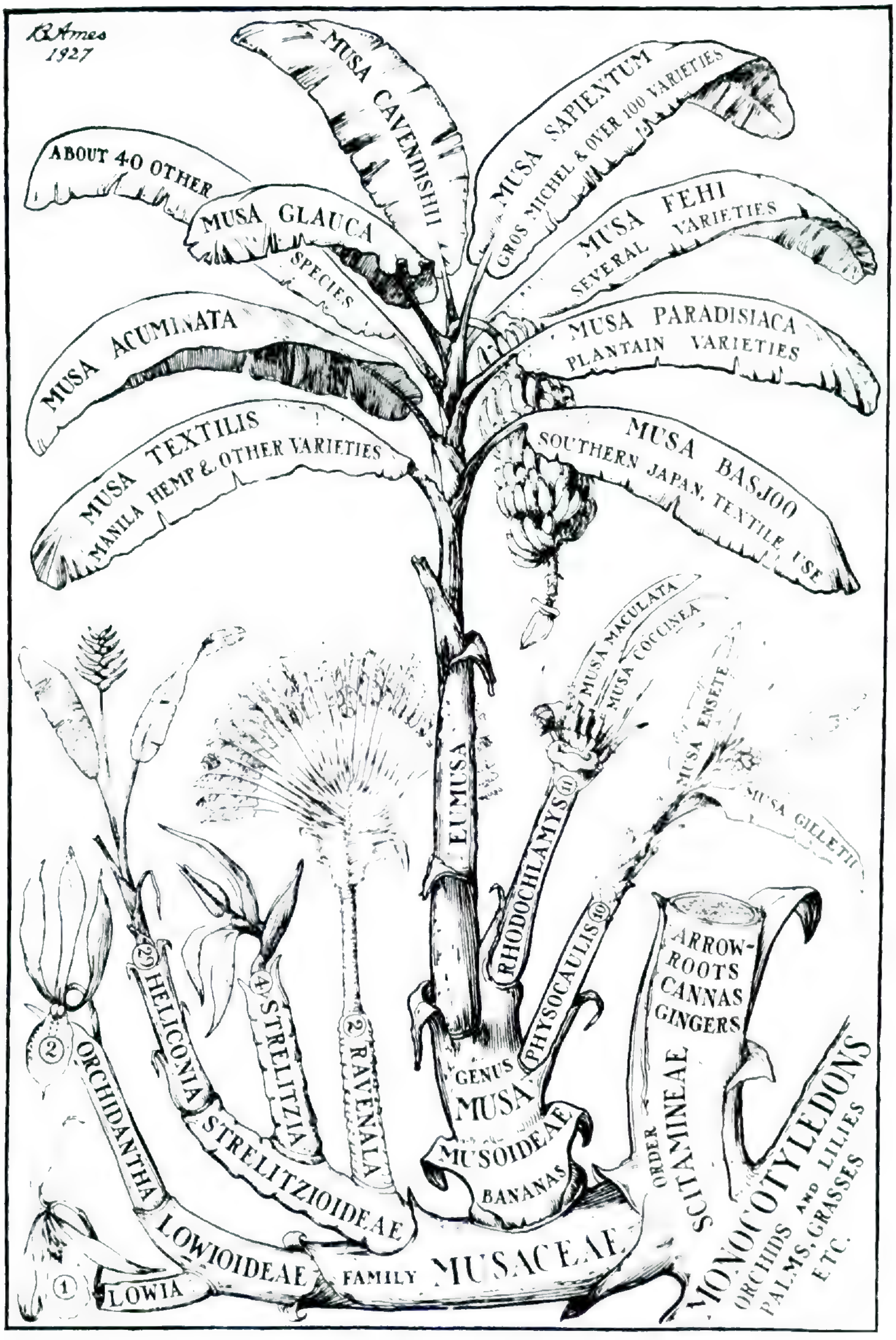

FIGURE 2. "Rhizogram" of the families of the Zingiberales. Rhizomatous patterns of growth are used to represent evolutionary branching relationships (from Reynolds, 1927).

(Heliconiaceae, Musaceae, and Strelitziaceae) with raphide sacs, symmetrical guard cells, and anomalous root structure (the last only in Musaceae and Strelitziaceae); Group 2 (Costaceae, Marantaceae, and Zingiberaceae) with asymmetrical guard cells, lack of raphide sacs, and normal root structure; Group 3 (Cannaceae) with symmetrical guard cells (variable), no raphide sacs, and normal root structure; and Group 4 (Lowiaceae) with raphide sacs, asymmetrical guard cells, and normal root structure.

Tomlinson then went on to discuss evolutionary trends in floral and vegetative characters as a basis for understanding the historical relationships of the four groups in the order. He concluded that the ". . . Strelitziaceae was the most primitive family within the Scitamineae, in the sense that its members possess the greatest number of primitive floral

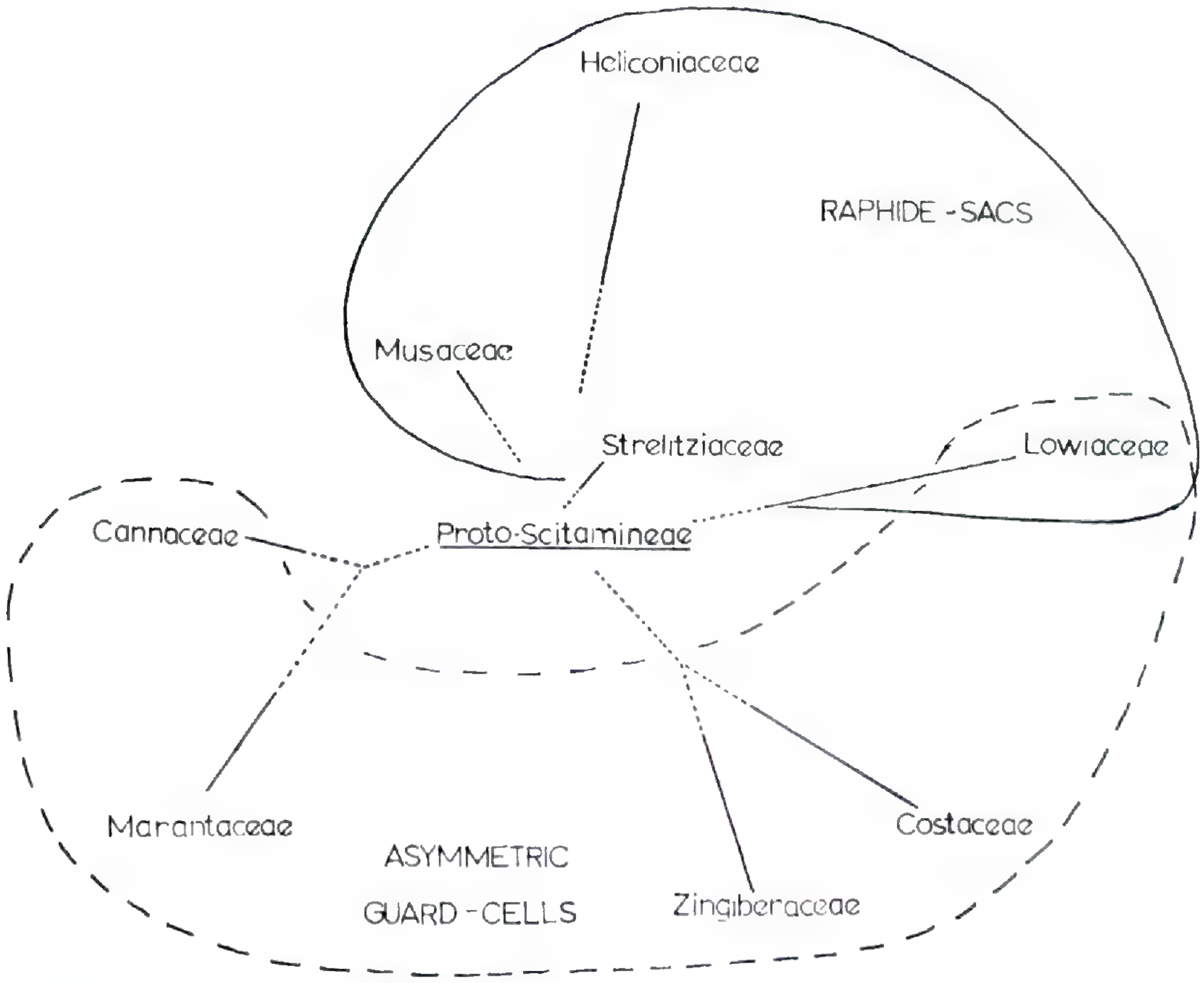

FIGURE 3. Tomlinson's two-dimensional concept of the evolutionary relationships of the eight families of the Zingiberales (from Tomlinson, 1962, his fig. 5).

features. Thus existing scitaminean flowers [and other vegetative and anatomical characters] can be regarded as derivative and advanced in varying degrees, compared with the strelitziaceous flower." Based on the assumption that the Strelitziaceae were the closest to a "proto-scitaminean" ancestor, Tomlinson diagrammatically represented the evolutionary relationships of the families (Fig. 3). However, the relationships depicted in his figure do not correspond to his four groups. In Group 1, the Heliconiaceae, Musaceae, and Strelitziaceae are positioned together in the figure, but each is on a separate line directly from the proto-scitaminean ancestor. Group 4, the Lowiaceae, is set in between Group 1 and the other families on its own distinctive line from the ancestor. Group 2 is divided into two separate lines. Two families of the group, Costaceae and Zingiberaceae, share a common branched line. The third family of Group 2, the Marantaceae, shares a common line with the only member of Group 3, the Cannaceae. The affinity of these last four families (plus the Lowiaceae) is depicted on the figure by a broken circle drawn around them, indicating the possession of asymmetrical guard cells (apparently erroneously including the Cannaceae). Likewise, the affinity of the families of Group 1 (plus Lowiaceae) is shown by a circle representing the presence of raphide sacs.

Tomlinson's publication on the Scitamineae, although somewhat ambiguous in the correspondence between the classification and its diagrammatic representation, was the first phylogenetic analysis of the eight families of the order that was based on a methodical examination of character distribution. His use of a priori evolutionary "trends" in floral traits (e.g., the designation of the strelitziaceous flower as primitive) to develop concepts of primitive and advanced states of other features may be criticized as a questionable method of character polarization. In addition, the relationships of the Musaceae, Heliconiaceae, and Strelitziaceae were never fully resolved in his work. The analysis, however, provided a concise rationale for linking the Marantaceae to the Cannaceae and the Zingiberaceae to the Costaceae, as well as for the distinct position in the order of the Lowiaceae.

Bisson et al. (1968), as the result of a lengthy caryological analysis of the Zingiberales, supported Tomlinson's (1962) inferences on the evolutionary relationships of the eight families. They informally proposed three suborders: (1) Strelitziaceae, Musaceae, and Heliconiaceae; (2) Zingiberaceae and Cosaceae; and (3) Marantaceae and Cannaceae; excluding the Lowiaceae due to the lack of adequate cytological data.

Dahlgren & Rasmussen's analysis. The most recent analysis of the phylogenetic relationships of

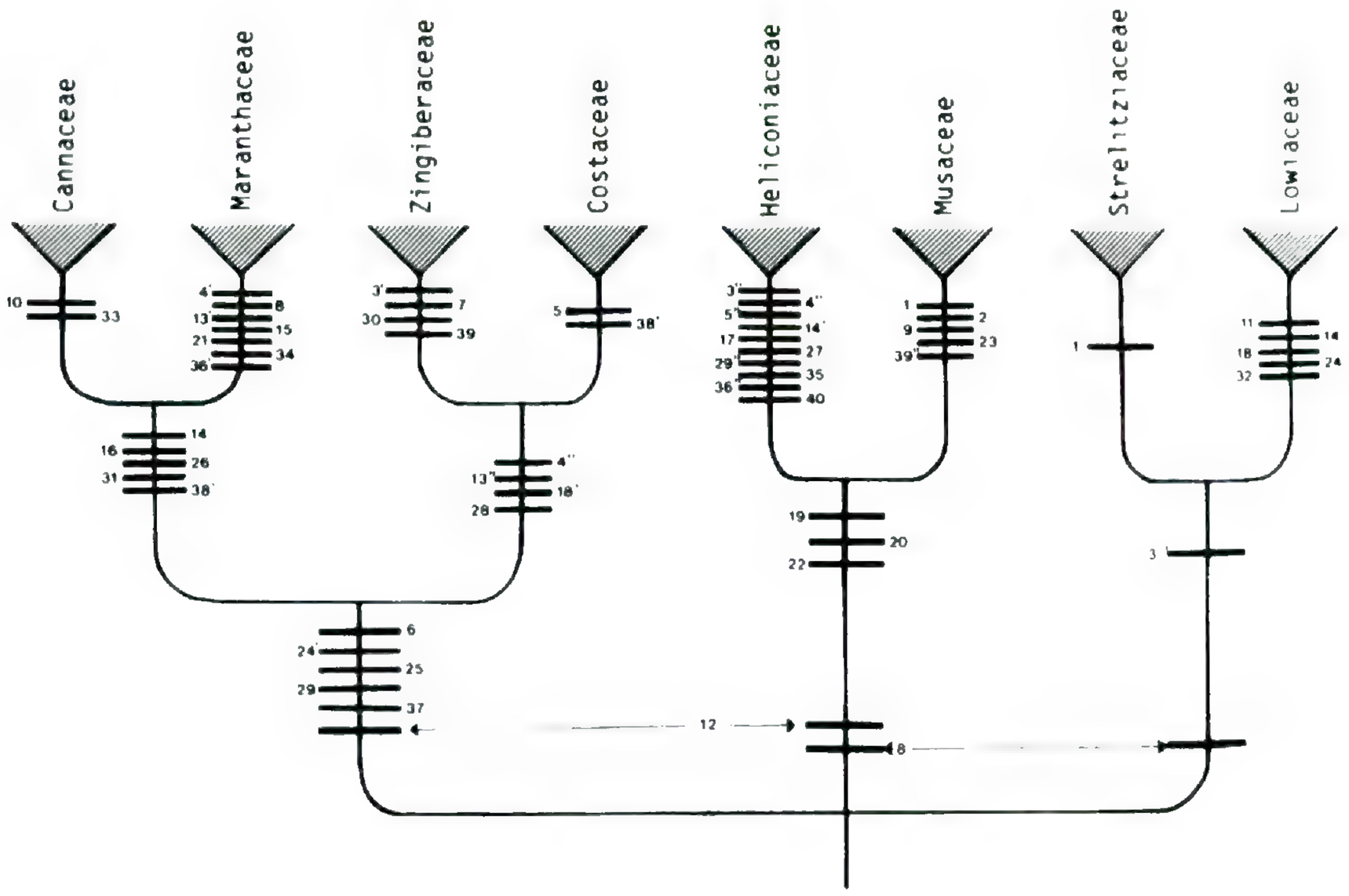

FIGURE 4. Cladogram of the Zingiberales resulting from the analysis of Dahlgren & Rasmussen (1983, their fig. 9).

the Zingiberales was by Dahlgren & Rasmussen (1983) in their publication on the evolution of the monocotyledons. They were not interested in the relationships of the order per se, but rather chose the group to demonstrate their method of cladistic analysis, which they advocated for an evaluation of the relationships of the monocotyledons as a whole. They selected the Zingiberales, accepting the eight families proposed by Nakai (1941), as an example "because of its unchallenged status as a monophyletic group . . . ."

Dahlgren & Rasmussen followed the basic procedures of Hennigian phylogenetic systematics by (1) selecting an outgroup, (2) polarizing characters of the ingroup based on the states present in the outgroup, and (3) grouping taxa according to shared derived character states (synapomorphies). They recognized that no unequivocal outgroup could be selected for the Zingiberales, but chose their Melliniflorae (discussed earlier) as the best possible outgroup. The morphological and anatomical characters described by Tomlinson (1962, 1969) provided the basis for the 40 two-state character set for the analysis. Their cladogram was constructed by "hand" according to a method described in the paper.

The best-defined section of the resulting cladogram (Fig. 4) was the monophyletic "ginger group" (Zingiberaceae, Costaceae, Marantaceae, and Cannaceae) united by the lack of raphide sacs, single fertile stamen, and abundant perisperm. Two pairs of sister groups within the ginger group were also each defined by several apomorphies: the Costaceae + Zingiberaceae by the fused staminodes; the Cannaceae + Marantaceae by the asymmetric flowers, bisporangiate anther, and specialized petaloid staminodes. Within the remaining four families of the order (the "banana group"), the Musaceae and Heliconiaceae were shown to be sister taxa based on the unique presence of the perianth tube, and the Strelitziaceae and Lowiaceae were united by their distichous phyllotaxy. However, due to the conflict presented by the distribution of two characters (terminal inflorescences and stegmata), some doubt was expressed as to whether the banana group formed a separate clade distinct from the ginger group. The thick-walled silica cells (stegmata) shared by the four banana families suggests that they are a monophyletic group. The presence of a terminal inflorescence in the Heliconiaceae, Musaceae, and the members of the ginger group unite those taxa. Dahlgren & Rasmussen considered the stegmata as the "more significant synapomorphy" and hence supported the monophyly of the banana group.

Dahlgren & Rasmussen's phylogeny of the Zingiberales does not conflict significantly with the scheme proposed by Tomlinson (1962). Both analyses accepted the two sister-group relationships within the ginger group (Marantaceae + Cannaceae; Costaceae + Zingiberaceae), and both considered the relationships of the four families of the banana group as somewhat unresolved. The monophyly of the four families of the ginger group is strongly supported by Dahlgren & Rasmussen. They also provided evidence for uniting as sister groups

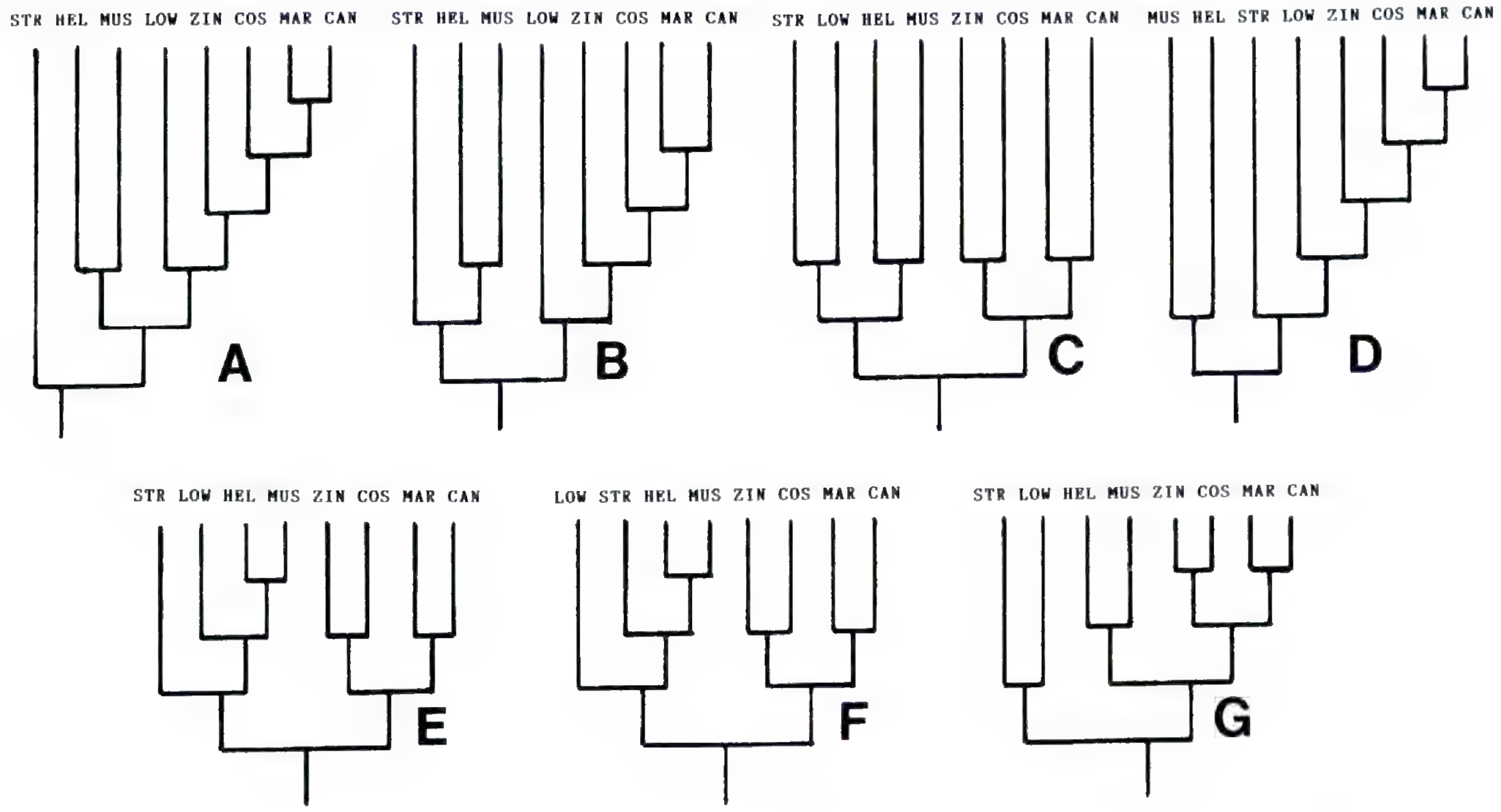

FIGURE 5. Seven equally parsimonious trees from Analysis One in which the character set of Dahlgren & Rasmussen (1983) was used.

the Heliconiaceae and Musaceae as well as the Lowiaceae and Strelitziaceae, but questioned the strength of this evidence. Their analysis is more explicit than Tomlinson's in its statements on the cladistic relationships of the families and the characters that define the monophyletic groups. Neither of the investigations suggested any new formal ranks.

Because of the formalized, explicit construction of the cladogram of Dahlgren & Rasmussen, it is possible to follow clearly their methods and provide a critique of the phylogeny. A close look at their data matrix reveals several problems, inconsistencies, and unnecessary characters in the analysis. Several of the 40 two-state characters used to construct the cladogram were coded incorrectly (e.g., characters 4 and 5: "uniseriate" is confused with "unicellular" trichomes; character 23: free median petal is found in the Musaceae and in the Strelitziaceae; character 30: all staminodes fused is an autapomorphy for the Costaceae, not the Zingiberaceae). Sixteen characters are coded (in some cases incorrectly) as being present in one family only, i.e., as autapomorphies for the terminal taxa, and therefore are of no value in determining relationships among the taxa (character 2: pseudobulbs; character 7: oil cells; character 9: articulated lacticifers; character 10: mucilage canals; character 11: axillary inflorescence; character 15: two-flowered inflorescences; character 17: resupinate flowers; character 21: corolla tube; character 23: free median petal; character 27: median stamen of outer whorl missing; character 30: all staminodes fused; character 32: hypanthiumlike neck on ovary; character 33: petaloid style; character 34: less than three fertile locules per ovary; character 35: basal placentation; character 40: schizocarp). Of course autapomorphies are of critical importance in defining the monophylesis of the terminal taxa, but they provide no information on cladistic relationships. Another problem with the character analysis is the coding of characters that are variable or polymorphic within taxa (e.g., character 8: stegmata; characters 11, 12: inflorescence type; characters 24, 27: stamen number; character 34: number of locules per ovary). Polymorphic characters can be legitimately used in cladistic analysis if evidence is provided for designating which of the states is plesiomorphic in the taxon. Dahlgren & Rasmussen did not provide this information. Finally, misinterpretation of some character state homologies (especially in perianth features; see below) led to inaccurate coding in several taxa.

The most significant deficiency of the phylogeny is the lack of any demonstration that the arrangement of taxa and characters in the cladogram is the most logically acceptable or parsimonious one. No justification was provided as to why this cladogram is the best representation of the relationships of the taxa based on the distribution of the available characters. To test the hypothesis that the cladogram presented by Dahlgren & Rasmussen is the most parsimonious, the same 24 characters (the 16 autapomorphies listed above were omitted) with

no recording or changes in polarization were reanalyzed using a computer-assisted maximum parsimony method (D. Swofford's PAUP program; see below). This method for inferring phylogenies, which places no restrictions on character state changes and estimates minimum length trees, is based on the same principles as the method used by Dahlgren & Rasmussen. Seven equally parsimonious cladograms (each with the same number of character state changes) were found (Fig. 5). The topology of each of the seven cladograms, which included the arrangement(s) presented by Dahlgren & Rasmussen (Fig. 5C, G), differed significantly in the relationships of the eight families. The sister-group relationships of the Heliconiaceae + Musaceae and the Marantaceae + Cannaceae were the only two consistencies in all seven of the cladograms. These results indicate that the analysis by Dahlgren & Rasmussen was not only incomplete, but that the character set they used is not sufficient (with the included inaccuracies) to determine unambiguously the phylogenetic relationships of the families of the Zingiberales.

The Phylogeny of the Zingiberales

The phylogenetic analysis performed by Dahlgren & Rasmussen (1983) was the first attempt to infer historical relationships of the eight families of the Zingiberales using the methods of phylogenetic systematics. However, as pointed out above, their results are suspect due to certain flaws in the analysis. Nevertheless, their cladistic methods were sound, and sufficient documentation was provided to repeat the analysis and test their hypothesis of the phylogeny of the Zingiberales.

An independent, original analysis of the Zingiberales using cladistic methods was initiated in the present investigation to clarify the conflicts, inconsistencies, and omissions of previous investigations. The aim of the study was to devise an unambiguous character set that would allow the estimation of a fully resolved cladogram to serve as the basis for a new hierarchical classification reflecting phylogenetic relationships.

MATERIALS AND METHODS

The eight families of the Zingiberales proposed by Nakai (1941) and accepted by Tomlinson (1962, 1969), Cronquist (1978, 1981), Dahlgren & Rasmussen (1983), and Dahlgren et al. (1985) were used as the operational taxonomic units in the present analysis. The autapomorphies listed earlier in the individual family descriptions are accepted as evidence for the monophyly of each of the families.

The characters used for inferring relationships were taken from a number of sources, including my own published and unpublished investigations. Lane (1955), Tomlinson (1956, 1959, 1961, 1962, 1969), and Dahlgren et al. (1985) were consulted for basic morphological and anatomical characters. Conflicts in the distribution of character states among these references were resolved by original observations where possible or by further reference to the works of other workers on specific families or characters, e.g., Humphrey (1896), Gatin (1908), Cheesman (1947), Holttum (1950, 1970), Simmonds (1962), Larsen (1966), Bisson et al. (1968), Mahanty (1970), Burtt (1972), Maas (1972, 1977), Wagner (1977), Williams & Harborne (1977), Goldblatt (1980), Olatunji (1980), Andersson (1981), Barthlott & Frölich (1983), Kirchoff (1983a, b, 1986), Kress (1984), and Rogers (1984).

In the Zingiberales, as is true in most plant groups, many characters are variable within the family. Unless the primitive state of a polymorphic character is known a priori, that character cannot be unequivocally coded and used in the analysis (Mickevich & Mitter, 1981). For this reason some variable characters were omitted from the analysis, e.g., cytology, stomatal type, septal nectaries, endosperm type, embryo shape, fruit type. Additional characters that may provide evidence on relationships, such as leaf flavonoids, are not known for all families (and are often variable in those taxa in which they are known) and were not included in the analysis in most cases. After attempting to assign states to more than 50 characters of the eight families, 32 characters (primarily floral morphology and vegetative anatomy) initially appeared unambiguous or "solid" enough to incorporate into the analysis (Table 2). All characters were defined to have two states to avoid the problems of devising a transformation series for multistate characters. Autapomorphies of the families, listed earlier in the family descriptions, were not included in the analysis.

Pollen characters were specifically omitted from the analysis even though a considerable amount is now known about the pollen of various families (e.g., Muller-Stoll, 1956; Saad & Ibrahim, 1965; Erdtman, 1966; Punt, 1968; Skvarla & Rowley, 1970; Kress et al., 1978; Stone et al., 1979, 1981; Kress & Stone, 1982, 1983; Hesse & Waha, 1983; Kress, 1986; Stone & Kress, unpublished). This information was not included because the cladogram resulting from the present analysis will

TABLE 2. Characters used in Phylogenetic Analyses Two and Three.

Character	Character states
1. Anticlinal walls of leaf epidermal cells	sinuous (0)[1] not sinuous (1)
2. Leaf guard cells	symmetrical (0)[1] asymmetrical (1)
3. Leaf adaxial hypodermis	≥1 cell layer (0)[1] 1 cell layer (1)
+4. Leaf longitudinal veins	independent of leaf surface (0)[1] attached to leaf surface (1)
+5. Leaf transverse veins	sheathed (0)[1] not sheathed (1)
+6. Transverse vein sheathing cells	thick-walled (0)[1] thin-walled (1)
7. Air canals in leaf axis	1 arc (0)[1] 2 arcs (1)
8. Root stele	polyarc (0)[1] with medullary vessels & phloem (1)
9. Raphide sacs	present (0)[1] absent (1)
10. Internal silica cell bodies—hat-shaped	absent (0)[1] present (1)
11. Internal silica cell bodies—trough-shaped	absent (0)[1] present (1)
12. Internal silica cell bodies—druse-shaped	absent (0)[1] present (1)
+13. Superficial cells with silica bodies	present (0)[1] absent (1)
14. Vessels	roots & stems (0)[1] roots only (1)
15. Phyllotaxy	spirally arranged (0)[1] distichous (1)
16. Flower shape	zygomorphic (0)[1] asymmetric (1)
+17. Sepals and petals fused into tube	no (0)[1] yes (1)
++18. All sepals	not fused (0)[1] fused at least at base (1)
++19. All petals	not fused (0)[1] fused at least at base (1)
+++20. Median petal	free (0)[1] fused to lateral petals (1)
21. Fertile stamen number	≥5 (0)[1] 1 (1)
22. Inner whorl median stamen	present/fertile (0)[1] absent (1)
23. Outer whorl median stamen	fertile (0)[1] not fertile (1)
24. Outer whorl median stamen	present (0)[1] absent (1)
25. Outer whorl lateral stamens	fertile (0)[1] staminodia (1)
26. Inner whorl lateral stamens	fertile (0)[1] staminodia (1)
27. Staminodes	not fused (0)[1] variously fused for most of length (1)
28. Anther(s)	tetrasporangiate (0)[1] bisporangiate (1)
29. Style	unmodified (0)[1] modified (1)
30. Ovule placentation	axile (0)[1] basal (1)
31. Aril	absent (0)[1] present (1)
+++32. Well-developed perisperm	absent (0)[1] present (1)
33. Endosperm	helobial (0)[1] nuclear (1)
34. Chalazosperm	absent (0)[1] present (1)

[1] Character state present in outgroup (Bromeliiflorae) and coded as primitive in the Zingiberales.
+ Omitted in Analysis Three.
++ Recoded in Analysis Three.
+++ Added to Analysis Three.

be used to infer the evolution of pollen wall structure in the Zingiberales in subsequent investigations (Kress & Stone, unpublished; see below).

The Bromeliiflorae of Dahlgren et al. (1985) was selected as the outgroup of the Zingiberales and the characters were polarized accordingly. The state common to the two groups was coded as the primitive state. For characters variable in the Bromeliiflorae (15, 17, 21), the state present in the Bromeliales (Bromeliaceae) was chosen as the primitive state in that superorder. In several cases, character states were unknown or nonexistent for some taxa and were coded as "missing."

The computer program PAUP (Phylogenetic Analysis Using Parsimony; Swofford, 1985) was used to infer the most parsimonious phylogeny. The "branch and bound" option (BANDB) of PAUP, which guarantees that the shortest trees will be found (if fewer than ten taxa), was used in conjunction with the ancestor rooting option (ROOT

TABLE 3. Taxon by character matrix for the eight families of the Zingiberales and 34 characters used in Phylogenetic Analyses Two and Three.

Family	Character																		
	1	2	3	4[1]	5[1]	6[1]	7	8	9	10	11	12	12[2]	13[1]	14	14[2]	15	16	17[1]
Lowiaceae	1	1	1	0	0	0	1	0	0	1	0	0	0	1	1	1	1	0	0
Musaceae	1	0	0	1	1	9	0	1	0	0	1	0	0	1	1	1	0	0	1
Heliconiaceae	0	0	1	0	0	1	1	0	0	0	1	0	0	1	1	1	1	0	1
Strelitziaceae	9	0	0	1	1	9	1	1	0	0	0	1	1	0	0	0	1	0	0
Zingiberaceae	1	1	1	1	0	1	0	0	1	0	0	9	0	0	1	0	1	0	0
Costaceae	1	1	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	0	0
Cannaceae	1	0	1	1	0	1	0	0	1	0	0	1	1	1	1	1	1	1	0
Marantaceae	0	1	1	1	0	1	0	0	1	1	0	0	0	1	0	0	1	1	0

0 = Primitive state.
1 = Advanced state.
9 = Missing character.
[1] = Omitted in Analysis Three.
[2] = Recoded in Analysis Three.
[3] = Added to Analysis Three.

= ANCESTOR) and the Farris method of HTU character state optimization (OPT = FARRIS).

Three separate analyses were run. The first was a test of the parsimony of the phylogeny derived by Dahlgren & Rasmussen (1983) and used the same characters (24, excluding the 16 autapomorphies) and polarity coding. The second and third analyses incorporated 34 independently derived characters (autapomorphies also excluded; Tables 2 and 3) and used the Bromeliiflorae as the outgroup.

After construction of the cladogram from the first independent character set (Analysis Two), character evolution was traced on the cladogram. As a result of the patterns revealed by the cladogram, each character was then reevaluated for defendable hypotheses of homology and accurate coding. Five characters (4: longitudinal veins; 5: leaf transverse veins; 6: transverse vein sheathing; 13: superficial cells with silica bodies; 17: sepal and petal fusion) could not be unambiguously coded because of variability in the outgroup, variability within families of the ingroup, or initial inaccurate morphological examination, and were omitted. Five characters (12: druse-shaped silica bodies; 14: vessels; 18: fusion of the sepals; 19: fusion of the petals; 23: outer whorl medium stamen) required recoding because of original mistakes in coding due to faulty literature reports. Two new informative characters (20: fusion of median petal; 33: perisperm) that were not included in the first original analysis were found. As a result of this character reevaluation, a second analysis (Analysis Three) was performed using the same PAUP options and a revised data set with characters omitted, recoded, or added as just described (29 total characters; Tables 2 and 3).

RESULTS

Analysis One: reevaluation of Dahlgren & Rasmussen study. The reanalysis of the character set of Dahlgren & Rasmussen, as discussed above, yielded seven equally parsimonious trees (Fig. 5), each with a total of 41 evolutionary steps (including 17 homoplasies; Consistency Index = 0.585). The seven trees included the two cladograms (Fig. 5C, G) of their analysis.

Analysis Two. The first of the independent analyses using the original set of 32 characters polarized with the Bromeliiflorae produced three equally parsimonious trees (Fig. 6A–C), each with 63 character state changes, including 31 homoplasies (Consistency Index = 0.508; *F*-value = 6.164–6.480). Each of these cladograms is fully resolved with all branching points dichotomous. The largest clade consistent in all three trees includes the Lowiaceae, Costaceae, Zingiberaceae, Cannaceae, and Marantaceae with the same sister group relationships in each tree. Autapomorphies of the Marantaceae–Cannaceae clade are asymmetric flowers (character 16), unfused staminodes (character 27), bisporangiate anthers (character 28), and a modified style (character 29). This clade is united with the Zingiberaceae by the absence of the median stamen in the outer staminal whorl (character 24). Synapomorphies of the clade formed by the Costaceae and Zingiberaceae–Cannaceae–Marantaceae are the absence of raphide sacs (character

TABLE 3. Continued.

Character																			
18	18^2	19	19^2	20^3	21	22	23	23^2	24	25	26	27	28	29	30	31	32^3	33	34
1	1	0	0	0	0	1	0	0	0	0	0	9	0	0	0	1	0	9	0
0	1	1	0	0	0	1	0	0	0	0	0	9	0	0	0	0	0	1	0
0	0	1	1	1	0	0	1	1	0	0	0	9	0	0	1	0	0	1	0
0	0	0	0	0	0	1	0	0	0	0	0	9	0	0	0	1	0	1	0
1	1	0	1	1	1	0	1	9	1	1	1	1	0	0	0	1	1	0	0
1	1	0	1	1	1	0	1	1	0	1	1	1	0	0	0	1	1	0	1
0	0	1	1	1	1	0	1	9	1	1	1	0	1	1	0	0	1	1	1
0	0	1	1	1	1	0	1	9	1	1	1	0	1	1	1	1	1	1	1

9), presence of a single fertile stamen (character 21), and staminodia in the lateral positions of the inner and outer staminal whorls (characters 25, 26). The Lowiaceae are united to this four-family clade by the asymmetric guard cells (character 2; lost in the Cannaceae) and the fused sepals (character 18; not shared by the Cannaceae–Marantaceae clade; this character was recorded for Analysis Three).

The variable lineages of the three equally parsimonious trees in Analysis Two are due to the unstable positions of the Musaceae, Heliconiaceae, and Strelitziaceae. In the first tree (Fig. 6A), the Musaceae and Heliconiaceae are sister groups united by the trough-shaped internal silica cell bodies (character 11) and the fused sepals and petals (character 17; this misinterpreted character is omitted in Analysis Three), as well as several other homoplasious characters (character 6: transverse vein sheathing cells; character 19: petals; character 31: no aril). In the other two trees (Fig. 6B, C) the Musaceae and the Strelitziaceae form a monophyletic lineage based on the shared unsheathed transverse leaf veins (character 5; variable and omitted in Analysis Three), the root stele with medullary vessels and phloem (character 8), and three homoplasious characters (character 3: multilayered leaf adaxial hypodermis; character 4: attached leaf longitudinal veins; character 22: inner whorl median stamen absent). No uniquely derived characters unite any of these lineages to the Lowiaceae–Costaceae–Zingiberaceae–Cannaceae–Marantaceae group in the three trees.

In all three of the trees, four characters change states between the outgroup (the Bromeliiflorae) and the common ancestor of the Zingiberales, and hence are additional synapomorphies of the order: two arcs of air canals in the leaf axis (character 7), distichous phyllotaxy (character 15), staminodia fused (character 27; not applicable to four of the eight families that possess one or no staminodium), and nuclear endosperm (character 33).

Among the three trees there are 11 uniquely derived character states, mostly floral traits, nine of which are common to all trees (character 9: raphide sacs absent; character 16: asymmetric flowers; character 21: one fertile stamen; character 24: outer whorl median stamen absent; character 25: outer whorl lateral stamens sterile; character 26: inner whorl lateral stamens sterile; character 27: staminodes not fused; character 28: bisporangiate anthers; character 29: modified style).

Analysis Three. In the reanalysis of the original 32 characters in which characters were omitted (characters 4, 5, 6, 13, 17), recoded (characters 12, 14, 18, 19, 23), or added (characters 20, 32), a single shortest tree (Fig. 7) was found with a total length of 53 steps, including 24 homoplasies (Consistency Index = 0.547; *F*-value = 4.939). Fifteen characters are uniquely derived (character 8: polyarc root stele; character 9: raphide sacs absent; character 16: asymmetric flowers; character 19: petals fused at base; character 20: median petal fused to lateral petal; character 21: one fertile stamen; character 22: inner whorl median stamen present; character 23: outer whorl median stamen not fertile; character 25: outer whorl lateral stamens sterile; character 26: inner whorl lateral stamens sterile; character 27: staminodes fused; character 28: anther bisporangiate; character 29: style modified; character 32: well-developed perisperm; character 33: helobial endosperm). The cladogram is fully resolved with all branching points dichotomous. The Cannaceae and Marantaceae form a terminal monophyletic lineage defined by asymmetric flowers (character 16), bisporangiate anthers (character 28), and a modified style (character 29). The Zingiberaceae and Costaceae, a second terminal group, are united by the uniquely

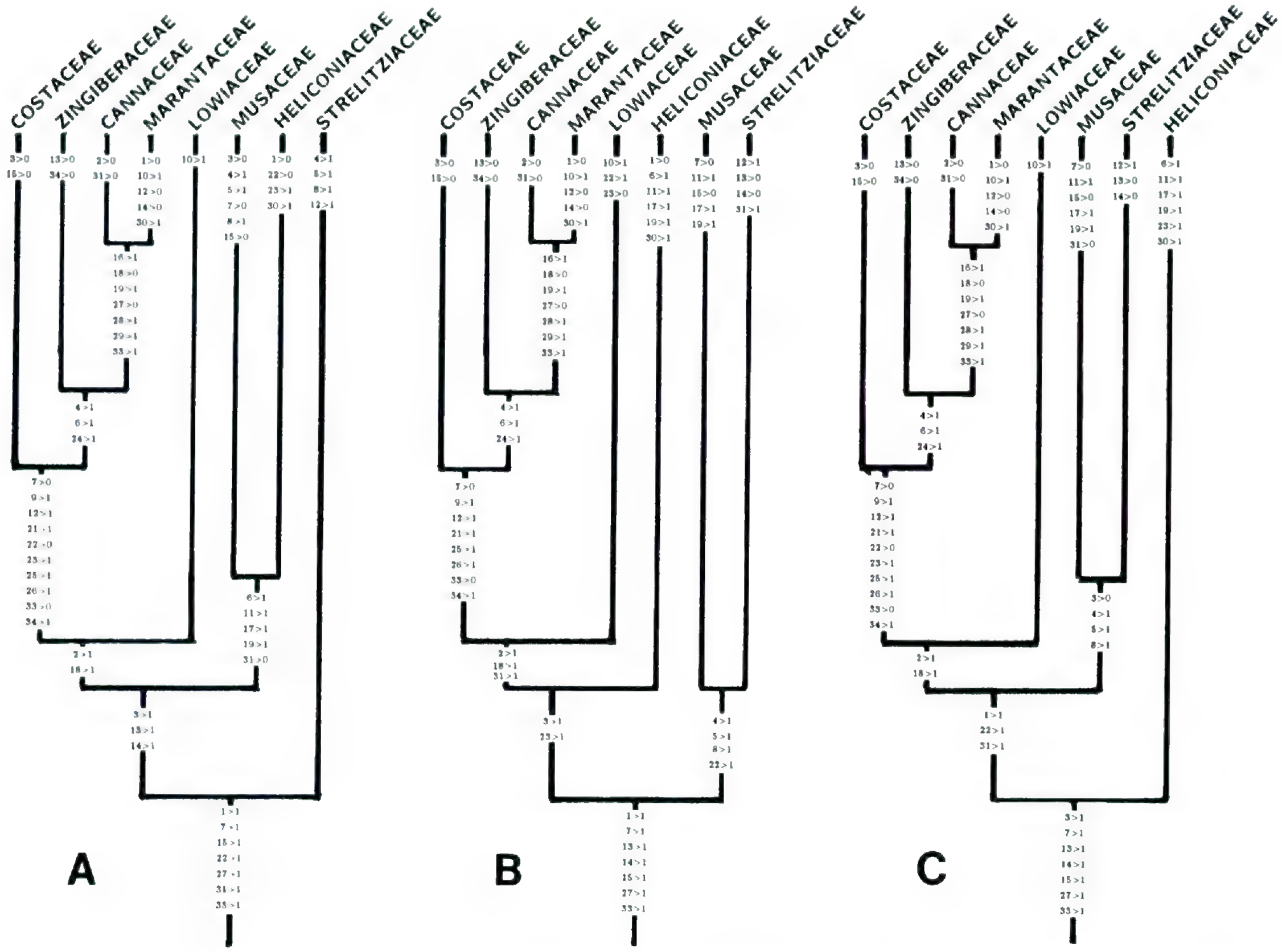

FIGURE 6. Three equally parsimonious cladograms of the Zingiberales resulting from Analysis Two. Numbers to the left of the arrows (>) refer to characters listed in Tables 2 and 3; numbers to the right of the arrows are apomorphic character states at that node.

derived fused staminodes (character 27) and helobial endosperm (character 33) as well as the homoplasious fused sepals (character 18; also in the Lowiaceae). Synapomorphies of the clade made up of these four families are the loss of raphide sacs (character 9), reduction in fertile stamens to one (character 21), staminodia in the lateral positions of the inner and outer whorls of stamens (characters 25, 26), and the well-developed perisperm (character 32). The single arc of air canals in the leaf axis (character 7; also in Musaceae), absence of the median stamen in the outer staminal whorl (character 24; regained in Costaceae), and the presence of chalazosperm (character 34; lost in Zingiberaceae) are homoplasies that also unite these families.

The Heliconiaceae are the sister group of the four-family "ginger group," sharing the basally fused petals (character 19), the median petal fused to the lateral petals (character 20), the presence of the median stamen of the inner staminal whorl (character 22), and the infertile stamen (i.e., staminode) in the median position of the outer staminal whorl (character 23), all of which are uniquely derived states on the tree. The Lowiaceae are joined to this five-family clade on the basis of the shared polyarc root stele (character 8), asymmetrical guard cells (character 2; symmetrical in the Cannaceae), and the one cell-layered leaf hypodermous (character 3; multiple layers in the Costaceae).

The sister taxon of the lineage formed by the Lowiaceae–Heliconiaceae–Costaceae–Zingiberaceae–Cannaceae–Marantaceae is the Strelitziaceae. Three homoplasious character states unite them: two arcs of air canals in the leaf axis (character 7; reversed to one arc in the ginger group), distichous phyllotaxy (character 15; reversed in the Costaceae), and the arillate seeds (character 31; lost in the Heliconiaceae and Cannaceae). These seven families share a common ancestor with the Musaceae, the eighth family of the order.

Five character states derived in the common ancestor are homoplasious in the order: nonsinuous anticlinal walls of the leaf epidermal cells (character 1; independently becoming sinuous in Heliconiaceae and Marantaceae), root stele with medullary vessels and phloem (character 8; polyarc in the Lowiaceae–Heliconiaceae–ginger group), vessels

restricted to the roots (character 14; vessels independently reappearing also in stems in the Strelitziaceae, Zingiberaceae, and Marantaceae), absence of the median stamen of the inner staminal whorl (character 22; regained in the Heliconiaceae–ginger group), and nuclear endosperm (character 33; helobial in Zingiberaceae–Costaceae).

DISCUSSION

Character analysis. Continual reassessment and reexamination of character state identification, distribution, and homology is the basis of any phylogenetic analysis. In the present investigation of the Zingiberales, the problem posed by the seven conflicting but equally parsimonious trees (Fig. 5) derived from the Dahlgren & Rasmussen character set was partly resolved by the reevaluation of their data. The three cladograms subsequently constructed in Analysis Two (Fig. 6) forced a further evaluation and reanalysis of the original characters leading to the single shortest tree produced in Analysis Three (Fig. 7).

Floral characters have presented much difficulty in assigning probable homologous states. For example, Dahlgren & Rasmussen (1983) mistakenly interpreted all three perianth characters that they used to unite the Musaceae and Heliconiaceae (their character 19: all sepals fused with petals into a tube; character 20: some sepals not part of perianth tube; character 22: petals part of a perianth tube). Although there is a "perianth tube" in both families, in the Musaceae it is made up of three fused sepals and two fused petals (the median petal free), while in the Heliconiaceae it is formed by two fused sepals and three fused petals (the median sepal is free). These "tubes" are certainly not homologous structures, and hence cannot unite the two families. In none of the families of the Zingiberales are "all sepals fused with [all] petals into a perianth tube" as they have defined their character number 19. The "corolla tube" (their character 21), assigned by Dahlgren & Rasmussen only to the Marantaceae, is also present in the Zingiberaceae, Costaceae, Cannaceae, and Heliconiaceae and is a synapomorphy of those five families according to Analysis Three.

The position in the two staminal whorls of the modified or missing stamens is also an important character that must be coded carefully. In the independent analyses conducted here, each position was designated as a separate character in assigning homologies. The sterile or lost stamen in the median position of the outer staminal whorl (characters 23, 24) and the fertile stamen in the

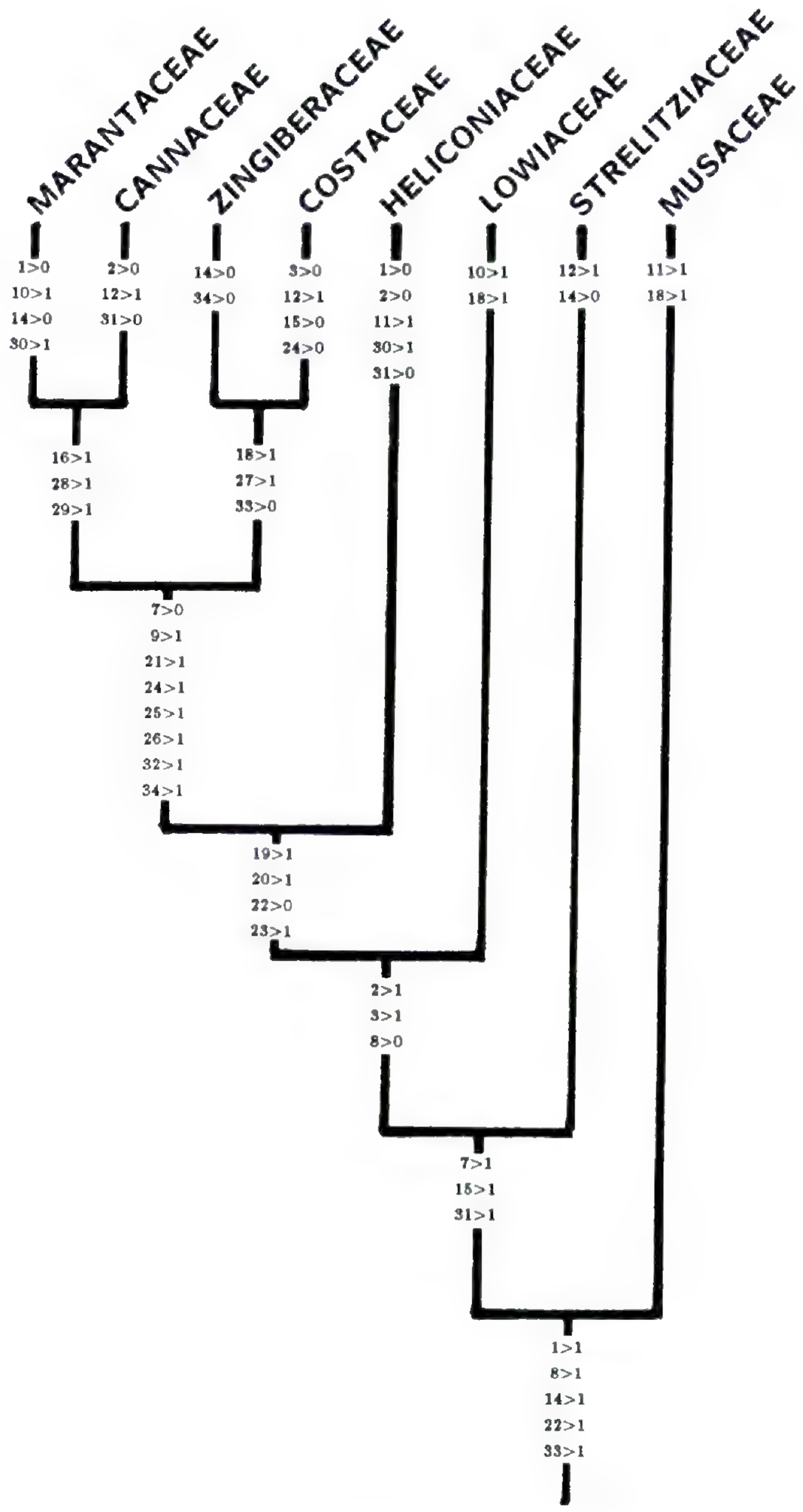

FIGURE 7. Most parsimonious cladogram of the Zingiberales resulting from Analysis Three. Numbers to the left of the arrows (>) refer to characters listed in Tables 2 and 3; numbers to the right of the arrows are apomorphic character states at that node.

median position of the inner staminal whorl (character 22) are thus interpreted as synapomorphies of the Heliconiaceae, Zingiberaceae, Costaceae, Cannaceae, and Marantaceae. The progressive evolutionary modification of the stamens into staminodes can be interpreted as beginning with the alteration of the outer median stamen in the Heliconiaceae followed by the outer and inner lateral stamens in the common ancestor of the other four families (the ginger group). The loss of the inner median stamen in the Musaceae, Strelitziaceae, and Lowiaceae is thus either an apomorphic loss in the common ancestor of the order that was regained in the common ancestor of the Heliconiaceae + ginger group, or three independent losses in those three families. The fact that at least one member

TABLE 4. Linnaean classification of the Zingiberales based on the cladistic relationships expressed in Figure 7 using the sequencing convention of Nelson (1972, 1974) and Wiley (1981).

Superorder Zingiberiflorae Dahlgren, Clifford & Yeo
Order Zingiberales Nakai
Suborder Musineae Kress, subord. nov.
Family Musaceae A. L. Jussieu
Suborder Strelitzineae Kress, subord. nov.
Family Strelitziaceae Hutchinson
Suborder Lowineae Kress, subord. nov.
Family Lowiaceae Ridley
Suborder Heliconineae Kress, subord. nov.
Family Heliconiaceae Nakai
Suborder Zingiberineae Kress, subord. nov.
Superfamily Zingiberariae Kress, superfam. nov.
Family Zingiberaceae Lindley
Family Costaceae Nakai
Superfamily Cannariae Kress, superfam. nov.
Family Cannaceae A. L. Jussieu
Family Marantaceae Petersen

of the Strelitziaceae (*Ravenala*) and possibly the Musaceae (*Ensete*; Dahlgren et al., 1985) possess this sixth stamen supports the second hypothesis and suggests the necessity of recoding character 21 (number of fertile stamens) in these two families.

In the Costaceae and the Zingiberaceae the staminodes are variously fused to each other (character 27), which was interpreted here as a synapomorphy of the two families. However, on closer inspection this fusion may not be homologous: all five staminodes are fused to form the labellum in the Costaceae, while only the two inner staminodes are united in the Zingiberaceae. Furthermore, several members of the Cannaceae show partial fusion of the staminodes, which in some cases can be fused basally to the corolla tube. If this character is homologous in these three families, then it is plesiomorphic in the ginger group (subsequently lost in the Marantaceae) and not a synapomorphy of the Costaceae–Zingiberaceae.

In the Marantaceae and the Cannaceae, the number of staminodes (three or four) varies among taxa. The presence of four staminodes was chosen as the state found in the common ancestor of these families (Fig. 1), which implies an independent loss of a staminode in each lineage. Additional investigations of the distribution and ontogeny of the various staminodes in the families of the ginger group are needed (e.g., Kirchoff, 1983a, b, 1986).

Only two of the 14 vegetative characters used in the third analysis are uniquely derived. The polyarc root stele (character 8) is interpreted as a synapomorphy of the Lowiaceae–Heliconiaceae–ginger group lineage, even though a similar feature is found in the outgroup. The absence of raphide sacs (character 9) evolved in the common ancestor of the ginger group and unites those four families. These two characters also furnished critical evidence for Tomlinson's (1962) recognition of natural groups in the Zingiberales. His third character, guard cells (character 2), is not uniquely derived in the present interpretation of the relationships.

Monophyletic groups. The results of the present analyses differ from previous classifications primarily in the recognition of the paraphyly of the group of "banana families" (Musaceae, Strelitziaceae, Heliconiaceae, and Lowiaceae). Earlier investigators (e.g., Bentham & Hooker, 1883; Schumann in Engler, 1900; Winkler in Engler & Prantl, 1930b; Lane, 1955; Tomlinson, 1962) united the genera of the banana group on the basis of the shared symmetrical guard cells, raphide sacs, and/or stamen number (five or six), all of which have been interpreted here as primitive (plesiomorphic) characters present in the common ancestor of the order. The inclusion of the members of these four families (or excluding Lowiaceae: Lane, 1955; Tomlinson, 1962) into the single family Musaceae s.l. has no cladistic basis.

The position of the Lowiaceae has always been controversial. Many unique floral and vegetative characters isolate this family from the other families of the order. In this analysis only the polyarc root stele provides evidence for its cladistic relationship to the Heliconiaceae and the ginger group.

The distichous phyllotaxy and the arillate seeds are the main features that unite the Strelitziaceae with the other six families of the order and exclude the Musaceae as the most "primitive" taxon. In this analysis the arborescent nature of the Strelitziaceae is a derived character and not a primitive feature as Tomlinson (1962) suggested.

The position of the Heliconiaceae as sister group to the four ginger families has not been acknowledged by any previous worker. The four floral synapomorphies shared by the Heliconiaceae and the ginger group provide evidence for uniting these families. The bananalike vegetative characters of *Heliconia* are plesiomorphies shared with the Musaceae and Strelitziaceae that have until now tended to obscure placement of this genus in the order.

The close relationship of the four families of the ginger group (Zingiberaceae, Costaceae, Cannaceae, and Marantaceae) has always been recognized (e.g., Tomlinson, 1962; Dahlgren et al., 1985), and the monophyly of this family group is supported

TABLE 5. Phylogenetic key to the order Zingiberales based on Figure 7.

1a. Lacticifers present; flowers unisexual, plants monoecious. (*Cellulae lactiferae praesentes; flores unisexuales, plantae monociae.*) ..... Suborder Musineae (Musaceae)
1b. Lacticifers absent; flowers bisexual 2
2a. Root stele with medullary vessels and phloem; stem woody; two lateral petals fused to enclose anthers. (*Radicis stela vasibus medullosis et phloemate instructa; caulis lignosus; petala duo lateralia connata, antheras includentia.*) ..... Suborder Strelitzineae (Strelitziaceae)
2b. Root stele polyarc; stem not woody; two lateral petals not so fused 3
3a. Sepals fused to form a solid tube; petals not fused; median petal free, forming labellum; median stamen of outer whorl fertile; median stamen of inner whorl absent. (*Sepala connata, tubum solidum formantia; petala non connata; petalum medianum liberum, labellum formans; stamen medianum verticilli exterioris fertile, interioris absens.*) ..... Suborder Lowineae (Lowiaceae)
3b. Sepals not forming a solid tube; petals fused at least at base; median petal not forming labellum; median stamen of outer whorl modified, sterile; median stamen of inner whorl present 4
4a. Two arcs of air canals in leaf axis; raphide sacs present; fertile stamens 5; lateral stamens of inner and outer whorls fertile; perisperm absent (*Arcus duo canalium aeriorum in axe folii siti; saci raphidibus instructi praesentes; stamina quinque fertilia, lateralia verticillorum interiorum exteriorumque fertilia; perispermium absens.*) ..... Suborder Heliconineae (Heliconiaceae)
4b. One arc of air canals in leaf axis; raphid sacs absent; fertile stamen 1; lateral stamens of inner and outer whorls sterile; perisperm present. (*Arcus unus canalium aeriorum in axe folii situs; saci raphidibus instructi absentes; stamen singulum fertile; stamina lateralia verticillorum interiorum exteriorumque sterilia; perispermium praesens.*) ..... 5. Suborder Zingiberineae
5a. Flowers zygomorphic; sepals fused at base; style unmodified, situated between anther sacs; anther tetrasporangiate; endosperm helobial. (*Flores zygomorphi; sepala in base connata; stylus immutatus, inter sacos antherarum situs; anthera tetrasporangifera; endospermium instar Helobiarum.*) ..... Superfamily Zingiberariae
6a. Phyllotaxy distichous; aromatic oils present in vegetative body; inner lateral staminodes fused into a labellum ..... Zingiberaceae
6b. Phyllotaxy spirally arranged; aromatic oils not present in vegetative body; all staminodes fused into a labellum ..... Costaceae
5b. Flowers asymmetric; sepals free; style modified, separated from anther; anther bisporangiate; endosperm nuclear. (*Flores asymmetrici; sepala libra; stylus mutatus, ex anthera discretus; anthera bisporangifera; endospermium non cellulosum.*) ..... 7. Superfamily Cannariae
7a. Mucilage cells absent from stems; pulvinus present; sigmoid lateral veins with evenly spaced cross veins in leaves; terminal pairs of enantiomorphic flowers; inner stamens modified into cucullate and callous staminodes; style not petaloid; single ovule per locule ..... Marantaceae
7b. Mucilage cells in stems; pulvinus absent; lateral veins oblique in leaves; petaloid style; flower pairs not enantiomorphic; inner staminodes and style petaloid; multiple ovules per locule ..... Cannaceae

by a large suite of synapomorphies. The controversy over the recognition of the Costaceae as a separate family from the Zingiberaceae is not resolved except to show that these two families form a distinct monophyletic lineage not cladistically inconsistent with the recognition of a single family Zingiberaceae.

The cladograms presented here and the work by Dahlgren & Rasmussen (1983) provide the only explicit, fully resolved representations of the phylogenetic relationships of the Zingiberales. The consistencies and inconsistencies among these trees are an indication of the problems and complexities of character analysis and the resultant interpretation of sister-group relationships among the families. The only consistent lineages in all trees are the four families of the ginger group and the Cannaceae–Marantaceae.

A new classification of the Zingiberales. One of the goals of this investigation was to derive a new classification of the order that reflected cladistic relationships. A strict cladistic hierarchical classification based on Figure 7 would be very complex. Because of the paraphyletic nature of the banana families, five ranks would be required between the order and family levels, four of which would include only a single family. For this reason a modified classification based on the cladistic relationships but following the "sequencing convention" of Nelson (1972, 1974) and Wiley (1981) is suggested (Table 4). The sequencing convention allows mono-

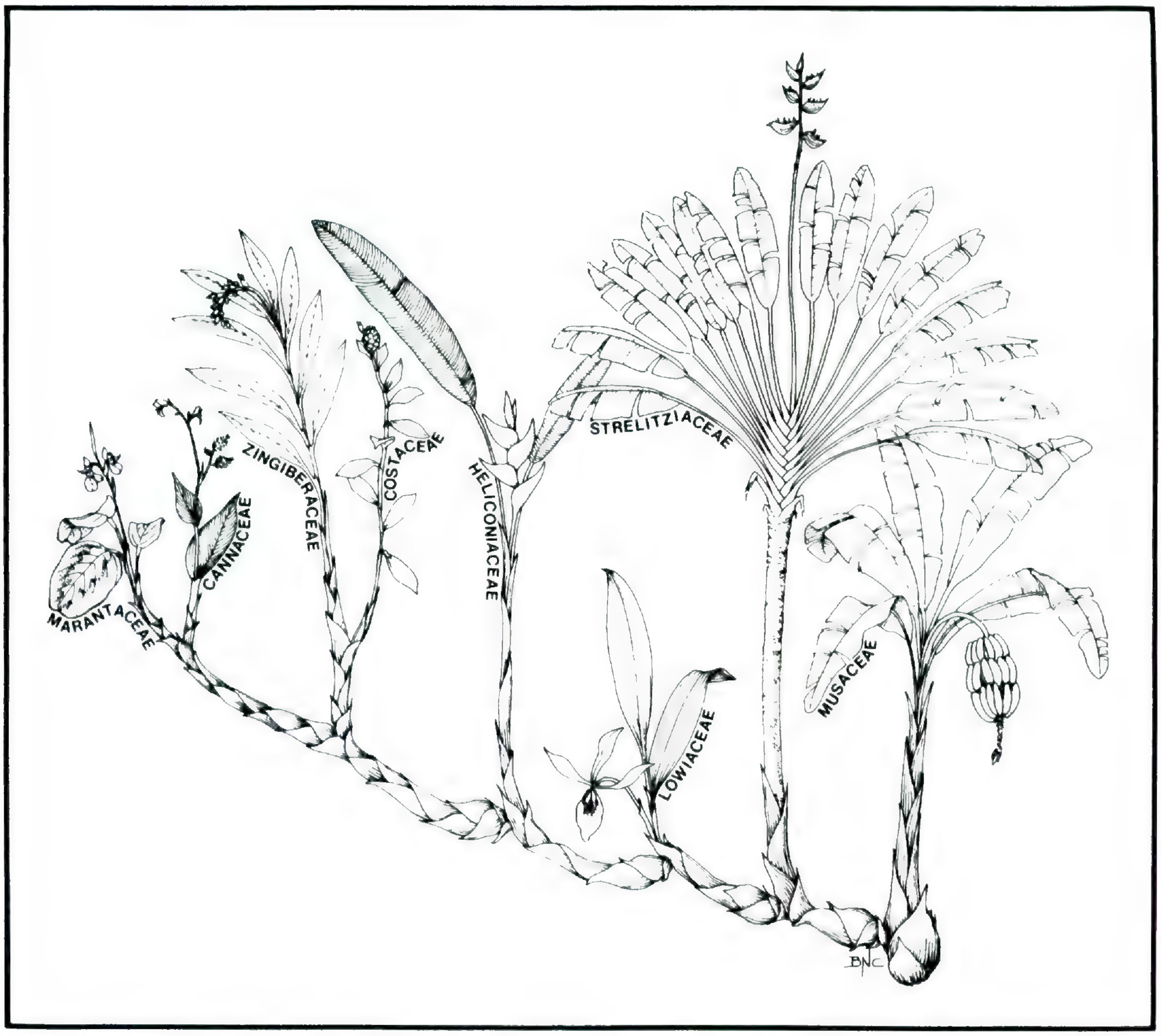

FIGURE 8. "Rhizogram" of the Zingiberales based on Analysis Three and Figure 7.

phyletic groups to be placed at the same rank (here suborders) and listed in the order of the branching sequence, thus reflecting the cladistic relationships without providing a separate categorical rank at each branching point. In the case of the Zingiberales this convention allows the retention of the eight terminal taxa at the rank of family and still provides a classification that exactly reflects the cladistic relationships. The classification depicted in Table 4 lists five new suborders, two new superfamilies, and eight families.

An alternative to erecting new taxa below the ordinal level is simply to list the eight families in order of their branching on the cladogram. Such a classification would cause confusion in reconstructing the relationships of the the families of the ginger group in which the Cannaceae–Marantaceae share a common ancestor not shared by the Zingiberaceae–Costaceae. The problem could be resolved by accepting the Zingiberaceae–Costaceae as a single family, as done in the past, which would then allow the legitimate listing of the seven families in order of their branching sequence. However, one might counterargue (with less conviction) that the Cannaceae and Marantaceae should also be combined into a single family, something most taxonomists would be reluctant to do.

CONCLUSIONS

The history of the classification of the Zingiberales shows that as information on new characters becomes available, new hypotheses on relationships among the families and taxonomic rank are proposed. In the present investigation, reevaluation of character state distributions and homologies coupled with the methods of phylogenetic systematics has provided a new classification based

on cladistic hypotheses. However, many phylogenetically useful characters in the Zingiberales remain to be studied carefully, appraised, and verified. Investigations of basic floral and inflorescence anatomy, morphology, and ontogeny, such as currently being carried out by Kirchoff (e.g., 1983a, b, 1986) and Kunze (e.g., 1985, 1986), will provide fundamental data to be incorporated in future analyses. Chemical data are still lacking for most of the families of the Zingiberales. No phylogenetic analysis utilizing molecular characters, such as chloroplast DNA restriction site variation, has yet been attempted on any taxa in the order.

In practice, most taxonomists can ignore the subordinal and superfamilial ranks in the classification proposed here if their goal is identification and placement of taxa only (see Table 5, Fig. 8). However, those biologists wishing to understand the evolution of taxa or characters within the order are dependent upon the phylogenetic information provided by the cladistic classification (Tables 4, 5). For example, as discussed earlier, pollen characters were not used in constructing the cladogram so that their evolution within the order could be inferred from the tree. The pollen wall of most of the families of the Zingiberales is characterized by a highly reduced exine and much-elaborated intine (Erdtman, 1966; Kress et al., 1978; Stone et al., 1979; Kress & Stone, 1982; Kress, 1986). As an exception the Costaceae and Zingiberaceae contain taxa with a well-developed exinous layer in the pollen wall (Punt, 1968; Stone et al., 1981; Kress, 1986). If the distribution of pollen wall features currently known for these families is superimposed on the cladogram of Figure 7, the simplest explanation of wall evolution is obvious. Reduction of the exine layer in the common ancestor of the order accounts for the presence of exineless pollen in six of the eight families. The much-thickened exine layer found in the pollen of the Costaceae and Zingiberaceae is therefore secondarily derived in the common ancestor of these two families, a hypothesis earlier proposed by Stone et al. (1981). The evolutionary explanation may be much more complicated than this, especially because the thickened exine is not found in all genera of the Zingiberaceae (Kress & Stone, unpublished). The important conclusion is that the presence of a thick exine in these families is not indicative of their "primitive" position in the order, but rather the independent evolution of the trait. The diversification of aperture type and the elaboration of the intine layer in the Zingiberales can be investigated in the same manner (Kress & Stone, unpublished). It is hoped that the present phylogeny of the Zingiberales will serve not only as a basis for the classification of taxa in the order, but also as a model for understanding character evolution in the monocotyledons.

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PHYLOGENY AND CLASSIFICATION OF THE HAEMODORACEAE[1]

Michael G. Simpson[2]

Abstract

A phylogenetic analysis of the monocot family Haemodoraceae is presented to assess the classification and interrelationships of tribes, genera, and species complexes and to determine patterns of evolutionary and biogeographic change. Evidence is reviewed for the monophylesis of the family (as here delimited) and of some family genera. In order to assign character polarities, two families, Philydraceae and Pontederiaceae, were hypothesized as closest outgroups based on presumed synapomorphies shared with the Haemodoraceae, including: (1) unifacial leaves (Philydraceae) and (2) verrucate pollen wall sculpturing and non-tectate-columellate exine structure (Pontederiaceae). A detailed analysis of the selection, definition, and coding of characters and character states is presented. Computer parsimony algorithms were used to construct most parsimonious trees. Utilizing all characters, including several for which polarity could not be determined, two equally most parsimonious cladograms were derived, differing only in the relative placement of the genera *Dilatris* and *Lachnanthes*. A cladistic analysis restricted to only those characters for which polarity could be determined yielded the same two equally parsimonious topologies; one in which correlated characters were scaled yielded one of the two topologies. Cladistic analyses support the monophylesis of the (herein defined) tribes Haemodoreae and Conostylideae. However, of the fourteen genera in the family, *Wachendorfia*, *Haemodorum*, and *Xiphidium* could not be a priori established as monophyletic, and the genera *Anigozanthos* and *Conostylis* are paraphyletic. Evolutionary events, as portrayed in the cladograms, are reviewed with emphasis on evolution of trichome anatomy, ovary position, ovule morphology, seed morphology, and chromosome number. Possible biogeographic scenarios support a Gondwanan origin for the Haemodoraceae with one major vicariance event occurring by the continental separation of present Antarctica from South America-Africa. With regard to interfamilial relationships, the Haemodoraceae are hypothesized as the sister group of the family Pontederiaceae, with both families more distantly related to the Philydraceae. Relationships to the Typhales, Bromeliaceae, and Zingiberales are still ambiguous, but the possibility of a close relationship of the Haemodoraceae-Pontederiaceae to the Zingiberales is considered.

The Haemodoraceae R. Br. are a monocot family of 14 genera and approximately 80 species with distributions in southern Africa, northern South America, Central America, Mexico, eastern North America, Australia, and New Guinea (Fig. 1). Members of the family are characterized as perennial, rhizomatous and stoloniferous or (more rarely) cormose to bulbous herbs with mostly basal to subbasal, equitant leaves and a terminal, generally cymose inflorescence (Geerinck, 1968, 1969a; Hutchinson, 1973; Robertson, 1976; present study). The leaves are "ensiform" (unifacial), resembling those of *Iris*. The flowers, typical of monocotyledons, are bisexual, with 6 tepals, 1–3–6 stamens, and a tricarpellate gynoecium developing into a capsular fruit. Flower symmetry is actinomorphic or zygomorphic; ovary position, ovule type, ovule number, and placentation are variable. Trichomes characteristically cover pedicels, hypanthia (if present), and outer perianth surfaces, often forming a dense tomentum. Several genera of the family possess a red sap in the roots and rhizome, accounting for the common name Bloodwort Family.

The Haemodoraceae have had some interesting economic uses. Several Australian species were used as a "nutritious food" by the aborigines, who roasted and consumed the "roots" (undoubtedly the rhizomes; Millspaugh, 1887). Narcotic effects have been attributed to the eastern North American *Lachnanthes caroliniana* (Lam.) Dandy (red root), the "roots" (again, likely rootstocks) of which were "esteemed as an invigorating tonic by the aborigines, especially the Seminoles, in whom it is said to cause brilliancy and fearless expression of the eye and countenance, a boldness and fluency of speech, and other symptoms of heroic bearing, with, of course, the natural opposite after-effects" (Millspaugh, 1887). Millspaugh also described a recipe for a red root tonic, with numerous medicinal

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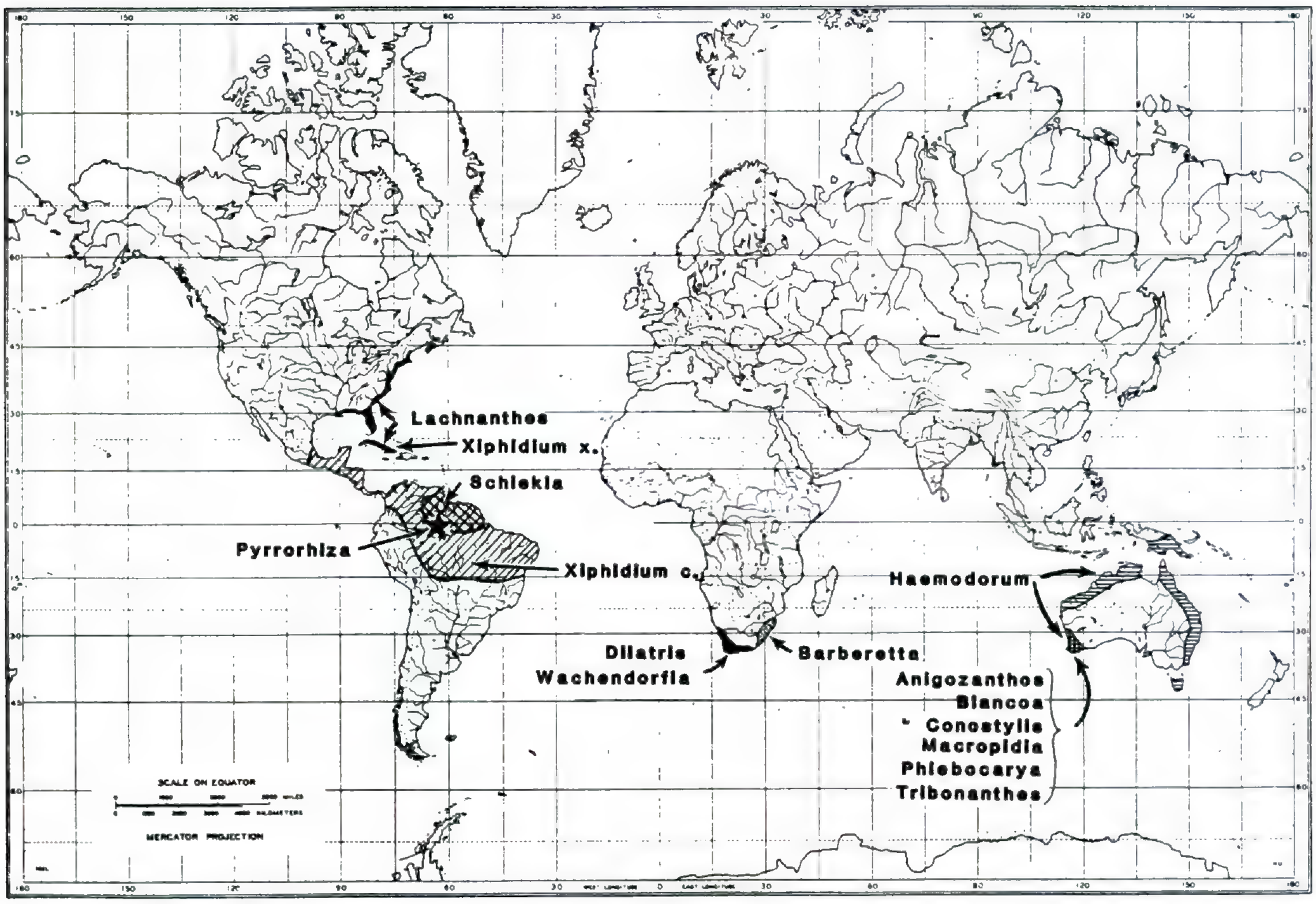


FIGURE 1. Geographic distribution of the genera of the Haemodoraceae. *Xiphidium x.* = *Xiphidium xanthorhiza*; *Xiphidium c.* = *Xiphidium coeruleum*.

benefits, including remedies for "rheumatic stiffness of the neck and shoulders," "typhus and thyroid fevers, pneumonia, various severe forms of brain disease, rheumatic wry-neck, and laryngeal cough." Charles Darwin (1872) in *The Origin of Species* (citing an example of selection) described the consumption of *Lachnanthes* by feral pigs in the southern United States; Virginia farmers had recorded that pigs with light-colored hair were poisoned by eating red root whereas dark-haired pigs were unaffected. Cooke & Edwards (1981) stated that this correlation between hair color and selective poisoning is presumed to be a photodynamic phenomenon, evidence being the induction of phototoxicity in microorganisms by extracts of *Lachnanthes* (Kornfeld & Edwards, 1972). The Australian *Haemodorum corymbosum* Vahl produces a red pigment (termed haemocorin), which has antitumor activity (Schwenk, 1962) and antibacterial activity (Narasimhachari et al., 1968). Several Australian members of the Haemodoraceae, including *Blancoa canescens* Lindl. (red bugles), *Haemodorum corymbosum* (blood root lily), *Macropidia fuliginosa* (Hook.) Druce (black kangaroo paw), *Tribonanthes* Endl. spp., and numerous species and forms of *Anigozanthos* Labill. (kangaroo paws, cats paws) and *Conostylis* R. Br., are horticulturally grown for their showy flowers (Dixon & Hopper, 1979). *Lachnanthes caroliniana* is listed as an agricultural pest, being a "rather aggressive weed in commercial cranberry (*Vaccinium macrocarpon*) bogs" (Robertson, 1976).

HISTORY OF CLASSIFICATION

As Geerinck (1968) and Robertson (1976) noted, the classification of the Haemodoraceae has been variable and uncertain, authors having proposed several different combinations of tribes and genera. Robert Brown (1810) first recognized the Haemodoraceae as a formal taxonomic unit composed of three southern African genera, *Dilatris*, *Lanaria*, and *Wachendorfia*, and four Australian genera, *Anigozanthos*, *Conostylis*, *Haemodorum*, and *Phlebocarya*. Diagnostic characteristics of the family were the six-parted, generally superior perianth (and thus an inferior ovary), capsular fruit, equitant leaves, and three or six stamens, if three then opposite the inner perianth lobes. Brown specifically distinguished the Haemodoraceae from the Iridaceae, members of which possess flowers with three stamens opposite the outer whorl of tepals.

TABLE 1. Classification of the Haemodoraceae sensu Bentham & Hooker (1883).

Tribe [Eu]Haemodoreae: perianth persistent; biseriate, the inner +/− enclosed by the outer; tube above the ovary absent or shortly developed. Stamens 3 or rarely 6.

1. *Haemodorum*
2. *Wachendorfia*
3. *Schiekia*
4. *Hagenbachia*
5. *Dilatris*
6. *Lachnanthes*
7. *Barberetta*
8. *Xiphidium*
9. *Lanaria*
10. *Phlebocarya*

Tribe Conostyleae: perianth persistent; lobes subequal, those of uniseriate species subvalvate. Stamens 6. Ovary locules with numerous ovules.

11. *Tribonanthes*
12. *Conostylis*
13. *Blancoa*
14. *Anigozanthos*
15. *Macropidia*
16. *Lophiola*
17. *Aletris*

Tribe Ophiopogoneae: perianth marcescent, persistent beneath the fruit; segments subequal, similar, flat. Ovary locules 2-ovulate. Pericarp after anthesis ruptured, not enlarged. Seeds berry-shaped, subglobose, extruded. Raceme unbranched. Flowers small.

18. *Peliosanthes*
19. *Ophiopogon*
20. *Liriope*
21. *Sansevieria*

Tribe Conanthereae: perianth at length around and above the ovary circumscissilly deciduous, segments subequal, similar or the exterior small and dissimilar, flat. Stamens or staminodes 6, equal or 1 or 3 of the other dissimilar; locules of anthers frequently terminally pored or rarely short dehiscent. Ovary locules (except *Odontostomum*) with numerous ovules. Capsules superior, loculicidally dehiscent. Flowers in loose panicles or rarely racemose or solitary.

22. *Conanthera*
23. *Cyanella*
24. *Zephyra*
25. *Tecophilaea*
26. *Odontostomum*

Subsequent to Brown's treatment, additional genera were included in the Haemodoraceae. Lindley (1830) placed the American genera *Lachnanthes*, *Lophiola*, and *Xiphidium* in the family. Endlicher (1836–1840) added the genera that Lindley contributed plus *Aletris*, *Androstemma*, *Blancoa*, *Hagenbachia*, *Tribonanthes*, *Vellozia*, and *Barbacenia* (the latter two genera of the tribe Vellozieae sensu Brown, 1810).

Bentham & Hooker (1883) provided the first critical treatment of the Haemodoraceae, considering the family to be intermediate between the Bromeliaceae and Iridaceae. Four tribes were designated: "Euhaemodoreae" (= Haemodoreae), "Conostyleae" (= Conostylideae), Ophiopogoneae, and Conanthereae (Table 1). Bentham & Hooker distinguished the tribes based on stamen number (3 vs. 6), perianth duration (persistent or deciduous), anther dehiscence (poricidal in the Conanthereae), ovary position (inferior vs. superior), and inflorescence type (Table 1). *Vellozia* and *Barbacenia* were excluded from the family as constituted by Endlicher, and placed in the Amaryllidaceae by Bentham & Hooker. The genus *Androstemma* was considered a generic section of *Conostylis*. Although subsequent treatments of the Haemodoraceae have varied considerably in the position and/or rank of certain genera and tribes, the four tribes proposed by Bentham & Hooker have remained essentially intact.

Pax (1888) in *Die natürlichen Pflanzenfamilien*, limited the Haemodoraceae to Bentham's tribe (Eu)Haemodoreae with the deletion of *Lanaria* and *Phlebocarya* and the addition of *Pauridia* (Table 2). According to this treatment, the Conostylideae (= Bentham's Conostyleae minus *Aletris* and plus *Lanaria* and *Phlebocarya*) and Conanthereae (minus *Odontostomum* of Bentham's classification) were transferred to the Amaryllidaceae, subfamily Hypoxidoideae, with the tribes Alstroemerieae and Hypoxideae. The tribe Ophiopogoneae was placed in the Liliaceae. Thus, of the original four tribes of Bentham, Pax considered only two, Conantherereae and Conostylideae, to be closely related. Ballion (1894) transferred the genera of the Haemodoraceae, sensu Pax, to the Amaryllidaceae. He argued that the Haemodoraceae are an artificial taxon essentially indistinguishable from members of the Liliaceae and Amaryllidaceae. Pax (1930) and Pax & Hoffmann (1930) did not support Ballion's view and made no changes in the group's classification relative to the previous edition.

Hutchinson (1934, 1959) advanced an original classification of the family. He united the Haemodoreae and "Conostyleae" (= Conostylideae) as two tribes of the Haemodoraceae, considering the family (as defined) to be a natural assemblage; and he treated the tribe Conanthereae of Bentham & Hooker (1883) as a distinct family, the Tecophilaeaceae (Table 3). Hutchinson classified the Haemodoraceae with five other families in the order Haemodorales, considering the group to be intermediate to the Amaryllidaceae and Orchidaceae. The Tecophilaeaceae, however, were placed in the Liliales and thought to be rather distantly related to the Haemodoraceae. In his third edition, Hutchinson (1973) added the newly discovered South American *Pyrrorhiza* (Maguire & Wurdack, 1957) to the tribe Haemodoreae.

Subsequent treatments of the Haemodoraceae have continued to vary with regard to tribal interrelationships and generic placement. Melchior

TABLE 2. Classification of the Haemodoraceae and Amaryllidaceae, subfamily Hypoxidoideae sensu Pax (1888).

Haemodoraceae

1. *Haemodorum* Sm.
2. *Barberetta* Harv.
3. *Hagenbachia* Nees
4. *Dilatris* Berg.
5. *Lachnanthes* Elliott
6. *Wachendorfia* L.
7. *Schiekia* Meissn.
8. *Xiphidium* Aubl.
9. *Pauridia* Harv.

Amaryllidaceae subfamily Hypoxidoideae

Tribe Alstroemerieae

1. *Alstroemeria* Blh.
2. *Bomarea* Mirb.
3. *Leontochir* Philippi

Tribe Hypoxideae

1. *Curculigo* Gartn.
2. *Hypoxis* L.

Tribe Conanthereae

1. *Conanthera* Ruiz & Pav.
2. *Cyanella* L.
3. *Zephyra* D. Don
4. *Tecophilaea* Bert.

Tribe Conostylideae

1. *Lanaria* Ait.
2. *Phlebocarya* R. Br.
3. *Macropidia* Drummond
4. *Tribonanthes* Endl.
5. *Lophiola* Ker
6. *Blancoa* Lindl.
7. *Conostylis* R. Br.
8. *Anigozanthos* Labill.

(1964) grouped the tribes Haemodoreae, Conostylideae, and Conanthereae as the Haemodoraceae, thus mirroring (with the exception of tribe Ophiopogoneae) Bentham's classification. In the most recent classification of the family, Geerinck (1969a) essentially concurred with Hutchinson in recognizing two tribes: Haemodoreae (10 genera) and Conostylideae (3 genera) (Table 4). Geerinck's system differs from that of Hutchinson in removing *Lanaria* and *Hagenbachia* from the family (to status "incertae sedis"), transferring *Lophiola* from the Conostylideae to the Haemodoreae, treating *Blancoa* as a section of the genus *Conostylis* and treating *Macropidia* as section of *Anigozanthos*. As a result of a multivariate morphometric analysis of *Macropidia fuliginosa* and 12 species of *Anigozanthos*, however, Hopper & Campbell (1977) argued for the reinstatement of *Macropidia* as a distinct genus.

The interfamilial classification of the Haemodoraceae has also been variable. Hutchinson (1973) classified the Haemodoraceae with the Apostasiaceae, Hypoxidaceae, Philydraceae, Taccaceae, and Velloziaceae in his order Haemodorales. Cronquist (1981) placed the Haemodoraceae in the order Liliales of the subclass Liliidae, "near" the families Pontederiaceae, Cyanastraceae, Philydraceae, and Liliaceae. In contrast, Takhtajan (1980) grouped the Haemodoraceae, Hypoxidaceae, and Velloziaceae in the suborder Haemodorineae of the Liliales. The Haemodoraceae were grouped with the Philydraceae and Pontederiaceae by Dahlgren (1980) and by Dahlgren & Clifford (1982). More recently, Dahlgren & Rasmussen (1983) grouped the Haemodoraceae, Pontederiaceae, and Typhales (Typhaceae and Sparganiaceae) as a tritomy (sharing a presumably derived amoeboid tapetum) in their superorder Bromeliiflorae. The Philydraceae were treated as a more basal clade, united with the above in having distichous leaves. Dahlgren & Rasmussen also included the Bromeliaceae and Velloziaceae as basal clades of the Bromeliiflorae (see Interfamilial Classification).

OBJECTIVES

The primary objective of the present study is to assess the phylogenetic relationships of the Haemodoraceae. A detailed analysis of the characters possessed by taxa is included and the rationale for character coding is discussed. A phylogenetic analysis, using these data, is presented in an attempt to answer the following: (1) Are the Haemodoraceae monophyletic? (2) Are the genera in the family monophyletic? (3) What is the basis for the traditionally recognized tribes Conostylideae and Haemodoreae? (4) What monophyletic subgroups of genera are evident and what are the character changes evident from the cladistic analysis? (5) Can inferences be made as to biogeographic history

TABLE 3. Classification of the Haemodoraceae and Tecophilaeaceae sensu Hutchinson, 1934, 1959, 1973. *Pyrrhorhiza* added in 1973.

Haemodoraceae

Tribe Haemodoreae: "perianth-segments 2-seriate; tube very short or absent; stamens 3 or rarely 6"

1. *Barberetta*
2. *Dilatris*
3. *Haemodorum*
4. *Hagenbachia*
5. *Lachnanthes*
6. *Lanaria*
7. *Phlebocarya*
8. *Pyrrorhiza*
9. *Schiekia*
10. *Wachendorfia*
11. *Xiphidium*

Tribe Conostyleae: "perianth-segments 1-seriate, subvalvate; tube often fairly long and curved; stamens 6; flowers always tomentose or woolly"

1. *Anigozanthos*
2. *Blanca* (sic)
3. *Conostylis*
4. *Lophiola*
5. *Macropidia*
6. *Tribonanthes*

Tecophilaeaceae

1. *Conanthera*
2. *Cyanastrum*
3. *Cyanella*
4. *Odontostomum*
5. *Tecophilaea*
6. *Walleria*
7. *Zephyra*

TABLE 4. Classification of the Haemodoraceae sensu Geerinck (1969a).

Haemodoraceae

Tribe Haemodoreae: "flowers glabrous or with simple or glandular trichomes; tepals distinct or rarely basally connate; functional stamens 6 (in 2 whorls of 3) or 3 (the outer whorl absent or replaced by 2 staminodes); anthers nonappendicular at apex; ovary superior, half-inferior, or inferior"

1. *Barberetta*
2. *Dilatris*
3. *Haemodorum*
4. *Lachnanthes*
5. *Lophiola*
6. *Phlebocarya*
7. *Pyrrorhiza*
8. *Schiekia*
9. *Wachendorfia*
10. *Xiphidium*

Tribe Conostylideae: "flowers covered with simple or branched trichomes (rarely both); perianth tube present; stamens 6, in 2 whorls of 3; anthers sometimes appendiculate apically; ovary half-inferior or inferior"

1. *Anigozanthos* (including *Macropidia*)
2. *Conostylis* (including *Blancoa*)
3. *Tribonanthes*

Genera of uncertain affinities: *Hagenbachia* & *Lanaria*

of the Haemodoraceae? (6) What families are most closely related to the Haemodoraceae and what is the evidence for this relationship? (7) What is the position of the Haemodoraceae within the Bromeliiflorae (sensu Dahlgren & Rasmussen, 1983)?

MONOPHYLESIS OF THE HAEMODORACEAE

It is essential in a phylogenetic study to demonstrate that the group to be analyzed is monophyletic (in the sense of Hennig, 1966; equivalent to "holophyletic" of other authors), i.e., that it includes all and only all descendants of a common ancestor as evidenced by one or more synapomorphies. Despite past discrepancies in classification, the Haemodoraceae are recognized in the present study to comprise a natural, monophyletic group made up of 14 genera: *Anigozanthos*, *Barberetta*, *Blancoa*, *Conostylis*, *Dilatris*, *Haemodorum*, *Lachnanthes*, *Macropidia*, *Phlebocarya*, *Pyrrorhiza*, *Schiekia*, *Tribonanthes*, *Wachendorfia*, and *Xiphidium*. The primary evidence for the monophylesis of the family is chemical composition. The Haemodoraceae are chemically unique in being the only family of vascular plants to possess phenalenones (specifically "arylphenalenones," derivatives of 9-phenyl-1H-phenalen-1-one; Cooke & Edwards, 1981). These compounds are responsible for the floral pigmentation and/or red coloration prominent in the roots and rootstocks of family members. The occurrence of phenalenones was first reported in *Haemodorum corymbosum* Vahl by Cooke & Segal (1955), who named the isolated phenalenone glycoside "haemocorin." Subsequently, the following ten species in eight genera of the family have been found to possess phenalenones or derivatives thereof: *Haemodorum corymbosum*, *H. distichophyllum*, *Lachnanthes caroliniana*, *Phlebocarya ciliata*, *Wachendorfia paniculata*, *W. thyrsiflora*, *Xiphidium coeruleum*, *Anigozanthos rufus*, *Conostylis setosa*, *Macropidia fuliginosa* (Cooke & Edwards, 1981, and references therein). The eight genera not investigated to date for the presence of phenalenones are, in the author's view, very closely related to those that have been, as determined by morphological and palynological similarity; it is hypothesized that, when chemically analyzed, they will be found to have arylphenalenones as well. It should be emphasized that among all investigated flowering plants, arylphenalenones have been found only in the cited members of the Haemodoraceae. Phenalenones are otherwise biologically known only in four genera of the Hyphomycetes (Fungi Imperfecti) and in one genus of the Discomycetes (Ascomycotina); these, however, are synthesized by a different biochemical pathway (Cooke & Edwards, 1981) and are obviously not homologous with those of the

TABLE 5. Embryological characters of the Haemodoraceae and relatives.

Taxon	Tapetal type	Microspore division	Nucellus type	Documentation
Haemodoraceae				
Anigozanthos	Amoeboid	Successive	Crassinucellate	Stenar (1927)
Dilatris	Amoeboid	Successive	Crassinucellate	De Vos (1956)
Lachnanthes	Amoeboid	Successive	Crassinucellate	Simpson (1981, 1988)
Wachendorfia	Amoeboid	Successive	Crassinucellate	Dellert (1933); De Vos (1956)
Xiphidium	Amoeboid	Successive	Crassinucellate	Stenar (1938)
Bromeliaceae				
	Glandular	Successive	Crassinucellate	Dahlgren et al. (1985)
Cyanastraceae				
Cyanastrum	Glandular	Simultaneous	Crassinucellate	Fries (1919); Nietsch (1941)
Hypoxidaceae				
Hypoxis	Glandular	Successive	Tenuinucellate	De Vos (1948)
Pauridia	Glandular	Successive	Tenuinucellate	De Vos (1949)
Philydraceae				
Helmholtzia	Glandular	Successive	Crassinucellate	Hamann (1966)
Orthothylax	Glandular	Successive	Crassinucellate	Hamann (1966)
Philydrella	Glandular	Successive	Crassinucellate	Hamann (1966)
Philydrum	Glandular	Successive	Crassinucellate	Hamann (1966)
Pontederiaceae				
Eichhornia	Amoeboid	Successive	Crassinucellate	Banerji & Gangulee (1937); Schurhoff (1922)
Monochoria	Amoeboid	Successive	Crassinucellate	Banerji & Haldar (1942)
Sparganiaceae				
Sparganium	Amoeboid	Successive	Crassinucellate	Dahlgren & Clifford (1982)
Taccaceae				
Schizocapsa	Glandular	Simultaneous	Crassinucellate	Hakansson (1921)
Tecophilaeaceae				
Cyanella	Glandular	Simultaneous	Crassinucellate	De Vos (1950)
Odontostomum	Glandular	Simultaneous	Crassinucellate	Cave (1952)
Typhaceae				
Typha	Amoeboid	Successive	Crassinucellate	Dahlgren & Clifford (1982)
Velloziaceae				
Vellozia	Glandular	Successive	Tenuinucellate (Pseudocrassinucellate)	Schnarf (1931); Stenar (1925)

Haemodoraceae. Because of the uniqueness of these compounds and their restriction to the Haemodoraceae, their presence is hypothesized as a synapomorphy, uniting the family as a monophyletic group. Other major similarities that the 14 genera have in common are: (1) occurrence of a fibrous layer ("mechanischen Cylinder") in the stem (Schulze, 1893); (2) presence of unifacial leaves with paracytic stomata (Schulze, 1893; Stenar, 1927, 1938; Green, 1959; Simpson & Dickison, 1981; Simpson, unpublished); (3) common embryological development, including occurrence of an amoeboid tapetum, successive microsporogenesis, and crassinucellate ovules (Table 5, and references therein); and (4) a similar and intergrading non-tectate-columellate pollen exine wall structure (Simpson, 1983; see Character Analysis). However, there is no evidence that any of these features are synapomorphic for the Haemodoraceae; they may, however, be synapomorphic for two or more families within the complex (see Interfamilial Relationships).

The family Tecophilaeaceae have often been classified as the tribe Conanthereae of the Haemodoraceae, but they definitely do not belong in

the latter. All investigated members of the Tecophilaeaceae (delimited as the genera *Conanthera*, *Cyanella*, *Odontostomum*, *Tecophilaea*, *Walleria*, and *Zephyra*; Simpson, in press) differ from the Haemodoraceae in having: (1) bifacial leaves and anomocytic stomata (Schulze, 1893; Simpson, unpublished); (2) a glandular tapetum and simultaneous microsporogenesis (Table 5); (3) phytomelaniferous seeds (except *Walleria*; Huber, 1969); and (4) pollen grains with a foveolate to reticulate sculpturing, an apertural operculum (except *Cyanella orchidiformis*), and a tectate-columellate exine architecture with an inner endexinous layer (Simpson, 1985b). In addition, members of the Tecophilaeaceae lack fluorescent cell wall-bound compounds found in the Haemodoraceae (Harris & Hartley, 1980; see Outgroup Taxa). All the evidence suggests that the Tecophilaeaceae are comparatively distantly related to the Haemodoraceae.

The taxonomic placements of *Hagenbachia*, *Lanaria*, *Lophiola*, and *Pauridia* have been variable in past treatments. Each has been included in the Haemodoraceae by various authors (e.g., Pax, 1930; Hutchinson, 1973; Melchior, 1964; Geerinck, 1969a; see History of Classification). However, a major conclusion reached from the present study is that no synapomorphies are known that unite any of these genera with the Haemodoraceae. The South American *Hagenbachia brasiliensis* (monotypic in its genus) is undoubtedly a case of taxonomic misplacement. It clearly belongs as a species of the genus *Chlorophytum* of the Liliaceae, as Ravenna (1977) determined. Corroborating this is the fact that "*Hagenbachia*" differs from all Haemodoraceae in having a tectate-columellate exine wall (Simpson, unpublished) and lacks UV-fluorescent cell-wall-bound compounds (Simpson, unpublished).

The monotypic, eastern North American *Lophiola* (which resembles some Haemodoraceae in having unifacial leaves, a corymb of helicoid cymes, and tomentose flowers and inflorescence) differs from the Haemodoraceae in many respects, including: (1) absence of a stem fibrous layer ("mechanischen Cylinder"), absence of subsidiary cells, and differing trichome anatomy (Schulze, 1893; Simpson & Dickison, 1981); (2) reticulate pollen with a tectate-columellate architecture (Simpson, 1983; Zavada, 1983a); (3) glandular tapetal development (Simpson, 1981); (4) absence of the diagnostic arylphenalenones (Edwards et al., 1970); and (5) absence of UV-fluorescent cell-wall-bound compounds (Simpson, unpublished). Ambrose (1980, 1985) presented convincing evidence for the classification of *Lophiola* in the Liliaceae, Melanthioideae (= Melanthiaceae of Dahlgren & Clifford, 1982); there is no doubt that it belongs with at least some members of that group.

The monotypic South African genus *Lanaria* resembles members of the Haemodoraceae in having a corymb of helicoid cymes and in having multiseriate, dendritic trichomes remarkably similar to those of some Haemodoraceae (see Character Analysis). However, *Lanaria* shows many differences from the Haemodoraceae, including: (1) bifacial leaves without stomatal subsidiary cells (Schulze, 1893; Simpson, unpublished); (2) glandular tapetal development and simultaneous microsporogenesis (Table 5); (3) reticulate pollen grains with a tectate-columellate exine wall structure (Simpson, 1983); (4) phytomelaniferous seedcoat (Huber, 1969); and (5) absence of UV-fluorescent cell-wall-bound compounds (Simpson, unpublished). (*Lanaria* has not been investigated chemically for the presence of arylphenalenones.) Similarities between *Lanaria* and the Tecophilaeaceae have prompted some (e.g., De Vos, 1961, 1963; Dahlgren & Clifford, 1982) to include the genus in that family. However, Dahlgren (pers. comm.) argued for the recognition of a segregate family, Lanariaceae, with close affinities to the Tecophilaeaceae.

Finally, the monotypic southern African genus *Pauridia* (usually placed in the Hypoxidaceae but sometimes classified in the Haemodoraceae) differs from the Haemodoraceae in having: (1) bifacial leaves; (2) tenuinucellate ovules and a glandular tapetum (Table 5); (3) disulculate pollen grains with a tectate-columellate exine having an endexinous basal layer (Simpson, 1983); and (4) absence of UV-fluorescent cell-wall-bound compounds (Simpson, unpublished). *Pauridia* has not been investigated for the presence of arylphenalenones. No characters evidently unite *Pauridia* to the Haemodoraceae; the genus is here retained in the Hypoxidaceae.

Monophylesis of Family Genera

In a cladistic analysis all defined operational taxonomic units (OTUs) should either be monophyletic taxa, be split up into monophyletic groups, or have exemplar species assigned for them. Otherwise, it is possible that one or more species of previously circumscribed genus "A" may be more closely related to species of genus "B" than to other species of genus "A." In the Haemodoraceae, the monophyly of six genera—*Barberetta*, *Blan-*

coa, *Lachnanthes*, *Macropidia*, *Pyrrorhiza*, and *Schiekia*—is accepted by virtue of their being monotypic. (See Platnick, 1976, for an alternate view.) A review of the monophyly of the remaining eight genera is essential before a valid cladistic analysis can be undertaken.

The genus *Dilatris* (five species) is commonly distinguished from other family members by having an inferior ovary and one ovule per carpel. Each of these features are possessed by other members of the family and thus cannot be recognized as synapomorphies (being unique only in combination). *Dilatris* has a trichome type not found in other genera of the family (see Character Analysis), yet if the proposed evolutionary gradation of trichome types (Fig. 28) is valid, then it is possible that the trichomes of *Dilatris* may not be uniquely derived for the genus as a whole. A feature that may show synapomorphy for the genus is the presence of dotted glands in the distal region of tepals (see Fig. 73). These glands were observed in *D. pilansii* and *D. corymbosa* but were not found in species of any other genus in the family. It is hypothesized that these tepal glands are likely synapomorphic for the genus as a whole.

Haemodorum (20 species) has a semibulbous underground rootstock, which is almost certainly derived from a primitive rhizomatous rootstock, present in almost all other family members (of both tribes) and in outgroups. This type of rootstock may not be unique to *Haemodorum*, as three other genera have a cormose rootstock (see Character Analysis, *Stem type*). Most species of *Haemodorum* are glabrous, which itself may be synapomorphic for the genus. The trichomes observed in *H. spicatum* (see Character Analysis, *Trichome anatomy*; Fig. 13) may be homologous with the pilate trichomes found in several genera of the tribe; thus, vestiture may not be a reliable indicator of synapomorphy (and therefore monophylesis) for the species of *Haemodorum*. In view of these difficulties and because relatively few of the 20 species of *Haemodorum* were observed in this study, monophylesis cannot be established for the genus.

No evident synapomorphies occur for investigated species of the genus *Wachendorfia* (five species). Possible derived characters in *Wachendorfia*, relative to the family as a whole, include zygomorphy and one ovule per carpel. However, these features also occur in other genera of the family and cannot be recognized as synapomorphies for this genus. The distinctive perianth apertures in *Wachendorfia* are also found in the genus *Schiekia* (see Character Analysis, *Perianth apertures*; Fig. 51). Monophylesis of *Wachendorfia*, therefore, cannot be affirmed in the present study.

Xiphidium consists of *X. coeruleum* and *X. xanthorhiza*, which differ only in minor morphological features and are likely more closely related to one another than to any other genus. However, because no definitive synapomorphy is evident for *Xiphidium*, its monophyly cannot be affirmed.

Tribonanthes has a unique, "stem tuberous" rootstock present in all five species (Pate & Dixon, 1981). This rootstock type may be derived for the genus; however, a cormose stem type is present in other genera and could be indicative of a common evolutionary origin for them (see Character Analysis, *Stem structural type*). Species of *Tribonanthes* do, however, have one feature that is very likely unique for the genus: the presence of distinctive appendages arising from the connective of the anther (see Character Analysis, *Stamen connective appendages*; Fig. 59). This feature is accepted as an autapomorphy, and *Tribonanthes* is hypothesized to be monophyletic.

The three species of *Phlebocarya* are quite similar to one another, differing primarily in leaf shape and vestiture. The similarities among *Phlebocarya* species in inflorescence and floral morphology provide good evidence of their very close relationship. In addition, flowers of *Phlebocarya* have a unilocular ovary and epitropous ovules; these are unique within the Haemodoraceae and may be synapomorphies for the genus. Therefore, *Phlebocarya* is accepted as being monophyletic.

Conostylis is the largest genus in the family, with ca. 25 species. No feature appears to be synapomorphic for the genus. The species of *Conostylis* show considerable variability in vegetative and floral morphology. In fact, *C. androstemma* and *C. bealiana* have an elongate perianth tube very similar to and possibly homologous with that of the monotypic *Blancoa* (see Character Analysis, *Perianth tube*). Although much more detailed studies of this genus are needed to resolve its intergeneric relationships, it is very likely paraphyletic; there is no evidence that one or more species of *Conostylis* might not be more closely related to *Blancoa* or even to species of *Anigozanthos*.

Anigozanthos is the second largest genus in the family, with ca. 10 species. Species of *Anigozanthos*, together with the monotypic *Macropidia*, almost certainly constitute a monophyletic group. Both have zygomorphic perianth tubes derived via a unique mechanism (see Character Analysis, *Perianth splitting*; Figs. 53, 54). *Anigozanthos* differs from *Macropidia* in trichome color and in having either two or numerous ovules per carpel (as op-

posed to one per carpel in *Macropidia*). However, trichome color is quite variable among species of *Anigozanthos*, and ovule number is likely not a shared derived feature for the genus. Because the characters distinguishing *Anigozanthos* from *Macropidia* are variable or likely to be plesiomorphic, it is uncertain that *Anigozanthos* is monotypic; one or more species of *Anigozanthos* may be more closely related to *Macropidia* than to other species of *Anigozanthos*.

Thus, five of the eight nonmonotypic genera of the Haemodoraceae cannot be reasonably shown, by evidence of synapomorphy, to be monophyletic. In this cladistic analysis of the Haemodoraceae, the following exemplar species are designated for these five genera: *Haemodorum spicatum*, *Wachendorfia thyrsiflora*, *Xiphidium coeruleum*, *Conostylis androstemma*, *Conostylis aurea*, *Conostylis bealiana*, *Anigozanthos flavidus*, and *Anigozanthos rufus*. Wherever *Haemodorum*, *Wachendorfia*, and *Xiphidium* are used in the analysis, it should be assumed that only the species indicated above applies. For *Conostylis* and *Anigozanthos*, it should be kept in mind that very few of the species in the genera will be considered and that these are exemplars. Future studies considering all species of these genera will be needed to assess fully their phylogenetic relationships.

Outgroup Taxa

In the following cladistic analysis character state polarity of ingroup taxa was determined using outgroup comparison. This basically entails performing a cladistic analysis on the ingroup plus one or more closely related taxa (outgroups), which serve to root the cladogram. The plesiomorphic state for the ingroup (at the outgroup node; see Maddison et al., 1984) is that which yields maximum parsimony among ingroups and outgroups. The major difficulty in applying outgroup comparison, however, is in determining which taxa indeed share most recent common ancestry with the Haemodoraceae. As previously discussed (see History of Classification) the interfamilial classification of the Haemodoraceae has been quite variable, a number of families having been proposed as close relatives. Therefore, in the present study, every monocot family that has ever been classified with or considered closely related to the Haemodoraceae was assessed as a possible outgroup. These families are: Apostasiaceae, Bromeliaceae, Cyanastraceae, Hypoxidaceae, Philydraceae, Pontederiaceae, Sparganiaceae, Taccaceae, Tecophilaeaceae, Typhaceae, and Velloziaceae. A comprehensive analysis of the phylogenetic relationships of these families to one another is beyond the scope of the present investigation and will be pursued in the future. Selective features from the literature and from ongoing studies by the author were assessed in order to determine the most likely closest outgroups. It was hoped that at least the two closest outgroups could be identified, as a minimum of two outgroups is required for unequivocally assessing character state polarity (see Maddison et al., 1984).

Evidence for the sister group relationship of the Haemodoraceae comes mainly from studies of pollen wall ultrastructure (Simpson, 1983, 1987). All investigated members of the Haemodoraceae have a 1–3-layered, non-tectate-columellate exine structure, which is almost certainly derived among the monocotyledons as a whole (Simpson, 1983; see Character Analysis). In contrast, all investigated members of the Apostasiaceae, Bromeliaceae, Cyanastraceae, Hypoxidaceae, Philydraceae, Sparganiaceae, Taccaceae, Tecophilaeaceae, Typhaceae, and Velloziaceae have a typical tectate-columellate exine structure (Ayensu & Skvarla, 1974; Nilsson et al., 1977; Brighigna et al., 1981; Simpson, 1983, 1985a, b; Zavada, 1983b). A tectate-columellate exine structure is presumed to be a plesiomorphic condition among the monocots (Zavada, 1983b) and cannot be utilized to define monophyletic groups. Among the taxa previously proposed to be closely related to the Haemodoraceae, only the Pontederiaceae are similar in pollen ultrastructure. Several members of the Pontederiaceae possess an exine sculpturing and structure identical to that of members of the Haemodoraceae (Simpson, 1987; see Character Analysis, *Pollen sculpturing*, *Exine wall structure*). The palynological similarities between the Haemodoraceae and Pontederiaceae constitute excellent evidence for the close relationship of the two families and are hypothesized here as synapomorphies linking the Haemodoraceae and Pontederiaceae as sister taxa (Simpson, 1987).

Identification of the next most closely related outgroup of the Haemodoraceae-Pontederiaceae complex is rather uncertain, however. Dahlgren & Rasmussen (1983) proposed that the presence of an amoeboid tapetum in the Haemodoraceae, Pontederiaceae, Typhaceae, and Sparganiaceae constitutes a synapomorphy for these four families, uniting them as a monophyletic group within their Bromeliiflorae. However, because an amoeboid tapetum occurs in numerous other monocot taxa, its use as a synapomorphy for these families seems less than certain, particularly with respect to differing opinions as to the classification of the Ty-

phales (Typhaceae and Sparganiaceae). Details of leaf morphology may provide less ambiguous evidence. Of the possible outgroups considered, the Haemodoraceae are similar only to the Philydraceae, Pontederiaceae, Sparganiaceae, and Typhaceae in possessing distichous leaves, a feature that Dahlgren & Rasmussen (1983) considered synapomorphic for these families. Of these families, only the Haemodoraceae and Philydraceae have unifacial (= ensiform) leaves. The presence of unifacial leaves is generally considered to be apomorphic among the monocotyledons. Occurrence of such leaves in the Philydraceae and Haemodoraceae is tentatively hypothesized as synapomorphic for the two families and evidence for their recent common ancestry, especially in light of numerous other similarities of the two families (see below). The evolutionary directionality of this feature may need further consideration, as Walker (1989) considers unifacial leaves to be plesiomorphic for the monocots as a whole.

Several other features link the Haemodoraceae to the Philydraceae and/or Pontederiaceae (and in many cases to other families), but the relative ancestry of these characters is uncertain or nonconclusive in outgroup selection. For example, among all outgroup candidates, the Bromeliaceae, Philydraceae, Pontederiaceae, Sparganiaceae, and Typhaceae are similar to the Haemodoraceae in having fluorescent, lignin-precursor acids (ferulic, diferulic, and p-hydroxybenzoic) bound to unlignified cell walls (Harris & Hartley, 1980). In contrast, these bound acids are absent in investigated members of all other considered outgroup families (i.e., Hypoxidaceae, Taccaceae, Tecophilaeaceae, and Velloziaceae). The data base for this character is quite small. Only one to a few genera or species have been investigated for many monocot families, and numerous families have yet to be investigated at all. Dahlgren & Rasmussen (1983) hypothesized that the presence of these fluorescent cell-wall-bound acids is a derived feature within the monocots, since these compounds are lacking in presumably closely related dicotyledons. Although many more taxa need investigation with regard to this feature, and although its biochemical significance needs elucidation, the presence of these fluorescent cell-wall-bound acids seems to constitute good evidence for the close relationship of the above families (see Interfamilial Relationships).

In addition, among the possible outgroups, only investigated members of the Haemodoraceae, Philydraceae, Pontederiaceae, and Sparganiaceae possess a common anatomical feature: presence of distinctive placental sclereid idioblasts (work in progress; see Character Analysis, *Placental sclereids*). These compounds are present in members of the Zingiberaceae as well (see Interfamilial Relationships). Although few taxa in families other than the Haemodoraceae have been investigated for this feature, it appears to provide yet another piece of evidence linking the Haemodoraceae, Philydraceae, Pontederiaceae, and Typhales.

In summary, the Pontederiaceae are chosen as the hypothesized sister taxon to the Haemodoraceae because of a similar and hypothetically derived pollen wall structure. The identification of the next most closely related outgroup is less certain. The Philydraceae are tentatively selected as this next most closely related outgroup because of the occurrence of similar, presumably derived, unifacial leaves in the Philydraceae and Haemodoraceae. Both outgroup families show similarity to the Haemodoraceae in anatomy (placental sclereids) and chemistry (fluorescent cell-wall-bound compounds), further supporting a close relationship. Certainly, additional studies are needed to assess interfamilial relationships in the complex (see Interfamilial Classification). However, rather than treat these outgroup families as unresolved or polytomous (Maddison et al., 1984), the evidence seems strong enough to utilize the Philydraceae and Pontederiaceae as most closely related outgroups to the Haemodoraceae in ascertaining the directionality of character state transformations.

Character Analysis

The following is a list and discussion of those characters and character states thought by the author to be important in resolving intrafamilial relationships. It should be stressed that the initial character selection makes this study "subjective," as it does all taxonomic studies, whether phylogenetic or not. Only characters that show clear discontinuities between the states are included in the analysis. Included in the character analysis are: (1) selection of characters; (2) selection and definition of character states; (3) assessment of homology of characters and character states; and (4) assessment of polarity of character states based on comparison with the designated outgroups (Philydraceae and Pontederiaceae) or other criteria.

Both outgroups were treated as operational taxonomic units (OTUs) in the data matrix. Characters with common states in all members of the Haemodoraceae (characters 52–55) are included in the analysis only to establish relationships of the two outgroups to the ingroup. A given character was coded as missing data ("?" in the data matrix)

if the taxon is polymorphic for the character, if data are unknown (e.g., chromosome numbers of *Schiekia* and *Pyrrorhiza*), or if X-coding is used (see below). Multistate characters were initially coded as two or more binary characters for ease of discussion. Where a multistate morphocline is illustrated in the character analysis, a character number in brackets portrays a coding such that taxa possessing the character to the left of the arrow are coded as state "0" and those to the right are coded as state "1."

For certain characters, the "X character" method (Doyle & Donoghue, 1986) was utilized, which codes the character state for certain taxa as "X" (equivalent to missing data, "?," in the computer algorithm), allowing for either of two alternative state changes. This technique is valuable in that the number of characters assigned to a given transformation series (morphocline) may often be reduced, thus minimizing unintentional weighting and unintentional bias, e.g., with regard to uncertain patterns of evolutionary direction.

MATERIALS AND METHODS

For studies of floral trichome anatomy and perianth cell types, small pieces of tepals and pedicels were removed and mounted in 50% glycerin. Preparations were left unstained or were occasionally stained with 0.01% aqueous Toluidine blue. For studies of perianth aestivation, immature buds were embedded in paraffin, and serial cross sections were prepared according to standard anatomical technique (Johansen, 1940). For observations of placental cell types, ovaries of mature flowers were paraffin-embedded and longitudinal sections were prepared as above. All sections were stained with safranin, iron hematoxylin, and fast green. Line drawings were made using a Wild Heerbrugg brightfield microscope with camera lucida attachment. Photographs were taken with a Leitz Wetzlar or Nikon Microphot-FX photomicroscope using Panatomic X film (ASA 32).

Plant material was fixed in either formalin/acetic acid/alcohol (noted "FAA" below) or 4% gluteraldehyde ("GLUT" below). Some material ("DRIED" below) was obtained from herbarium sheets and reexpanded in Aerosol OT for 2–5 days, followed by several water rinses and then fixation in FAA. Materials and methods for the ultrastructural observations of pollen grains are discussed in Simpson (1983, 1985a, b, 1987). Documentation for the taxa studied in the present work is as follows (parentheses indicate herbaria that house vouchers):

HAEMORDORACEAE

Anigozanthos flavidus DC. "FAA"—*M. G. Simpson 24IX81J* (DUKE)

Anigozanthos rufus Labill. "FAA"—*M. G. Simpson 27IX81F* (SDSU)

Barberetta aurea Harv. "FAA"—*R. Ornduff 7661* (UC)

Blancoa canescens Lindl. "GLUT"—*M. G. Simpson 18IX81AA* (DUKE)

Conostylis androstemma F. Muell. "DRIED"—*S. R. Preif 1409* (K)

C. aurea Lindl. "FAA"—*M. G. Simpson 13IX81S* (SDSU)

C. bealiana F. Muell. "FAA"—*Arboretum, U.C. Santa Cruz, 3XI80*

Dilatris corymbosa Berg. "FAA"—*P. Goldblatt 3242* (MO)

D. pilansii Barker "FAA"—*P. V. D. Meriwe 30X81-2* (STEU)

Haemodorum simplex Lindl. "GLUT"—*M. G. Simpson 20IX81A* (DUKE)

H. spicatum R. Br. "FAA"—*M. G. Simpson 16IX81C* (DUKE)

Lachnanthes caroliniana (Lam.) Dandy "FAA"—*M. G. Simpson 14VI80A* (DUKE)

Lanaria lanata (L.) Dur. & Schinz "DRIED"—*R. D. A. Bayliss 4369* (US)

Lophiola aurea Ker-Gawler "FAA"—*M. G. Simpson 14VI80B* (DUKE)

Macropidia fuliginosa (Hook.) Druce "FAA"—*M. G. Simpson 18IX81DD* (DUKE)

Pauridia minuta (L.f.) Dur. & Schinz "DRIED"—*P. MacOwan & H. Bolus 291* (US)

Phlebocarya ciliata R. Br. "GLUT"—*M. G. Simpson 16IX81A* (DUKE)

P. pilosissima F. Muell. "FAA"—*M. G. Simpson 16IX81K* (DUKE)

Pyrrorhiza neblinae Maguire & Wurdack "DRIED"—*B. Maguire, J. J. Wurdack & G. S. Bunting 37222* (US)

Schiekia orinocensis (Kunth) Meisn. "FAA"—*B. Maguire 41569* (NY)

Tribonanthes australis Endl. "DRIED"—*A. J. Eames & A. T. Hotchkiss, 23VIII1953* (US)

T. variabilis Lindl. "FAA"—*M. G. Simpson 8IX81A* (DUKE)

Wachendorfia paniculata L. "FAA"—*P. V. D. Merwe 30X81-1* (STEU)

W. thyrsiflora L. "FAA"—*R. Ornduff 7691* (UC)

Xiphidium coeruleum Aubl. "FAA"—*J. M. MacDougal 1043* (DUKE)

HYPOXIDACEAE

Curculigo capitulata (Lour.) Kuntze "FAA"—*M. G. Simpson 29VI80* (FTG)
Hypoxis micrantha Pollard "FAA"—*M. G. Simpson 5V82A* (DUKE)

LILIACEAE TRIBE OPHIOPOGONEAE

Liriope muscari (Decne.) L. H. Bailey "FAA"—*M. G. Simpson 7VII81A* (DUKE)

PHILYDRACEAE

Helmholtzia acorifolia F. V. Mueller "FAA"—*M. G. Simpson 81-16A* (DUKE)
H. novo-guineensis (Krause) Skottsberg "DRIED"—*L. J. Brass 12859* (A)
Orthorthylax glaberrimus (Hooker fil.) Skottsberg "FAA"—*U. Hamann 1183* (Herb., U. Hamann, Berlin)
Philydrum lanuginosum Gaertner "FAA"—E. F. Constable; *U. Hamann 959* (NSW)
Philydrella pygmaea (R. Brown) Caruel "FAA"—*M. G. Simpson 28IX81A* (DUKE)

PONTEDERIACEAE

Heteranthera reniformis R. & P. "GLUT"—*M. G. Simpson 4VIII82A* (DUKE)
Pontederia cordata L. "GLUT"—*M. G. Simpson 4VIII82B* (DUKE)
Reussia rotundifolia (L.f.) Castell "DRIED"—*G. T. Prance 23284 & J. F. Ramos* (US)

SPARGANIACEAE

Sparganium eurycarpum Engelm. "FAA/GLUT"—*M. G. Simpson 21VI86A* (SDSU)

STRELITZIACEAE

Strelitzia reginae Ait. "FAA"—*M. G. Simpson 11XI86A* (SDSU)

TACCACEAE

Tacca integrifolia Ker.-Gawl. "FAA"—*M. G. Simpson 23V82* (Duke Univ. greenhouses 81-0379)

TECOPHILAEACEAE

Conanthera bifolia R. & P. "DRIED"—*E. P. Killip & E. Pisano 39690* (US)
C. trimaculata Don. "DRIED"—*C. Grandjot* (MO 1126476)
Cyanastrum cordifolium Oliv. "DRIED"—*B. O. Daramola 41029* (MO)
Cyanella alba L.f. "FAA"—*R. Ornduff 7463* (UC)
C. hyacinthoides L. "FAA"—*R. Ornduff 7501* (UC)
C. lutea L.f. var. *lutea* "FAA"—*R. Ornduff 7565* (UC)
Odontostomum hartwegii Torr. "FAA"—UCBG 53.845
Tecophilaea violiflora Bert. ex Colla. "DRIED"—*O. Buchtien 10VIII1895* (US)
Walleria mackenzii Kirk. "DRIED"—*J. Buchanan 1891* (US)
W. muricata N. E. B. "DRIED"—*N. C. Chase 5182* (MO)
Zephyra elegans D. Don. "DRIED"—*E. Werdermann 776* (US)

VELLOZIACEAE

Barbecenia seubertiana Goeth. & Henr. "FAA"—*Hatschbach 30095* (Duke Univ. greenhouses)

CHARACTER CODING

Character #1. Root and stem coloration. *Dilatris*, *Haemodorum*, *Lachnanthes*, *Pyrrorhiza*, *Wachendorfia*, and *Xiphidium* have a red, red-orange, or maroon coloration of the roots and underground stems (Thiselton-Dyer, 1896–1897; Adamson & Salter, 1950; Maguire & Wurdack, 1957; Geerinck, 1969a; Simpson, pers. obs.), accounting for the family name Haemodoraceae (Gr. *haima*, blood), the Bloodwort Family. This reddish coloration results from the presence of one or more forms of the distinctive class of chemical compounds, phenalenones. Although all investigated family members contain phenalenones (Cooke & Segal, 1955; Cooke et al., 1958; Cooke & Edwards, 1981; see Introduction), only the above six genera show red pigmentation in the roots and rootstocks. The possible adaptive significance of this coloration is unknown; it may simply be correlated with a high concentration of one or more forms of this class of compounds. The fact that these pigments are toxic to certain livestock, at least in *Lachnanthes* (see Characterization and Economic Importance), may be significant in this regard.

Character #2. Stem structural type. Most members of the Haemodoraceae have an elongate to congested, sympodially branched rhizome, commonly bearing proliferative stolons, although four genera deviate from the rhizomatous habit. *Pyrrorhiza*, *Tribonanthes*, and *Wachendorfia* possess

an underground corm (illustrated for *Wachendorfia* in Fig. 2). In *Tribonanthes* the corm (termed a "root tuber," sensu Pate & Dixon, 1981) develops from a downward-directed axillary bud which penetrates the outer scale leaves of the old corm (initially resembling a root); further growth results in the formation of a globose mass of tissue. *Pyrrorhiza* and *Wachendorfia* (Fig. 2) have a basal cluster of globose corms; it is not known whether they develop similarly to those of *Tribonanthes*. *Haemodorum* has a somewhat bulbous corm, not like a typical bulb, but consisting of an aggregate of the swollen, fleshy bases of primarily nonphotosynthetic leaves (Thiselton-Dyer, 1896–1897; Pate & Dixon, 1981; Simpson, pers. obs.). The bulbous corm of *Haemodorum* is tentatively coded as homologous to that of the above three genera. (*Barberetta* is somewhat intermediate between the rhizomatous and the cormose taxa, having short, horizontal, rather fleshy proliferative shoots; however, these are probably a slight specialization of the rhizomatous/stoloniferous habit and are not coded as evolutionarily intermediate to the cormose stem type.)

The hypothesized morphocline for stem structural types in the family is: [#2] RHIZOMATOUS ↔ CORM OR BULBOUS CORM. However, such a hypothesis seems to be very tentative. Deviations from a strictly rhizomatous stem habit likely have occurred secondarily more than once (e.g., via strong selective pressure for dormancy) and thus may not indicate homology.

Of the outgroups, a rhizomatous/stoloniferous stem is present in all members of the Pontederiaceae. In the Philydraceae three of the five species have a rhizomatous stem type, but *Philydrum lanuginosum* has a basal caudex (Dahlgren et al., 1985), and *Philydrella pygmaea* has corms similar to those of the cormose Haemodoraceae (Pate & Dixon, 1981; pers. obs.). Thus, the Philydraceae are coded as polymorphic for stem structural type. Interestingly, *Philydrella* is found with *Tribonanthes* (in southwest Australia); they occur together in similar habitats (low, winter-wet flats). It is probable, however, that the common stem habit of these two taxa is not by homology, but is the result of separate, secondary adaptations to a winter-wet, summer-drought environmental regime.

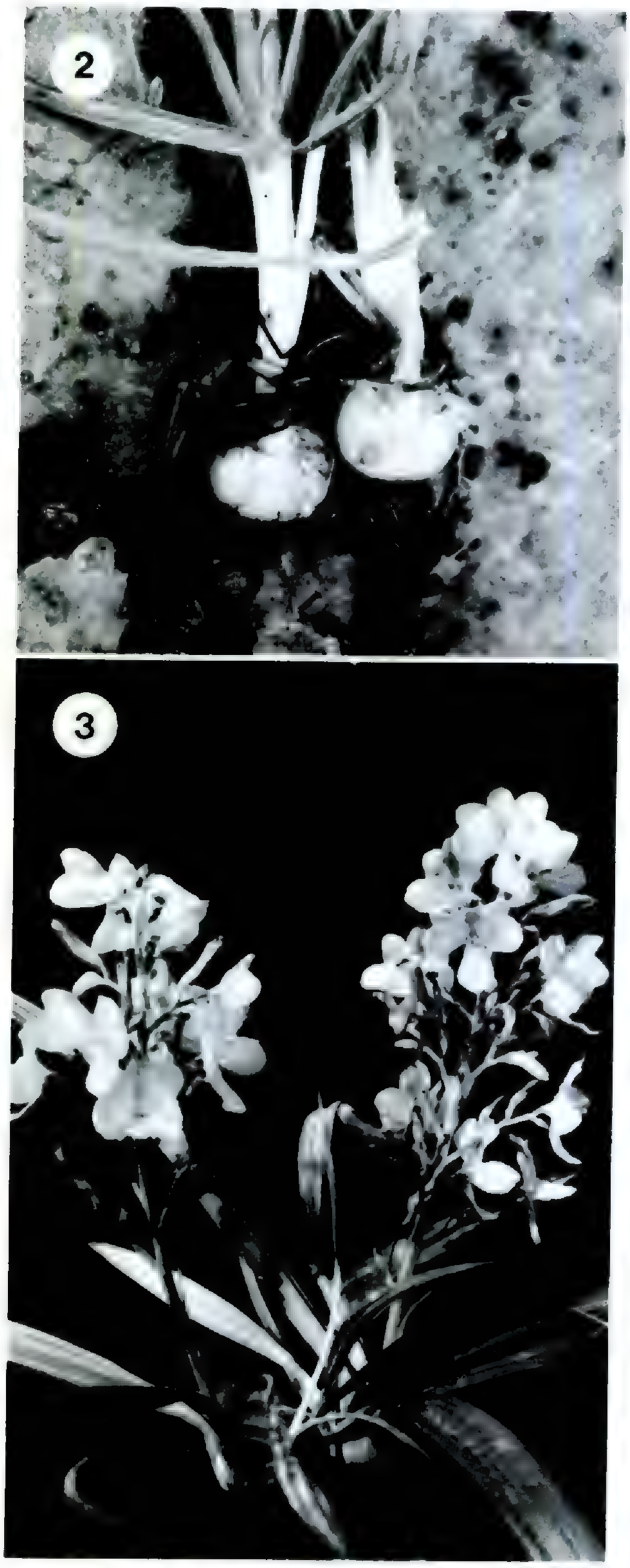
Character #3. Plicate leaves. *Barberetta* and *Wachendorfia* have longitudinally plicate leaves (Figs. 3–5), a condition found in no other member of the Haemodoraceae nor in any of the outgroups. (*Helmholtzia* of the Philydraceae has unifacial leaves with a pseudo-costa but no evidence of plication.) Plication in these two genera arises by the occurrence of longitudinal folding and development of tissue ridges opposite the major vascular bundles (Fig. 5). The presence of similar plicate leaves in *Barberetta* and *Wachendorfia* constitutes strong evidence for their common evolutionary origin within the Haemodoraceae and is coded as derived (from an ancestral leaf with smooth posture).

Characters #4–6. Inflorescence type. Inflorescences in the Haemodoraceae are quite variable, but most have a common theme, consisting of a network of helicoid cymes (e.g., Fig. 6) arranged as a panicle, raceme, corymb, or capitulum. The inflorescence of *Haemodorum* differs in being a raceme, panicle, or corymb of either flower pairs or cymules containing paired flowers. In addition, corymblike aggregates of bifurcate or trifurcate helicoid cymes occur in *Dilatris* and *Lachnanthes*, and bifurcate helicoid cyme aggregates (in the form of a raceme, panicle, corymb, or capitulum) occur in *Anigozanthos*, *Blancoa*, *Conostylis*, *Macropidia*, *Phlebocarya*, and *Tribonanthes*. *Barberetta* is unique in the family in having a simple raceme.

The possible evolutionary intergradation between these varied inflorescence types is uncertain. A coding of inflorescence types that may likely represent homologies in the family is related to the cyme unit itself rather than to the type of aggregation of these cyme units. The morphocline used in the present study is: CYME ABSENT ←[#4]→ CYME SIMPLE ←[#5]→ CYME BIFURCATE ←[#6]→ CYME BIFURCATE OR TRIFURCATE. In this morphocline only the simple raceme of *Barberetta* would be coded as lacking a cyme unit. The flower pairs or cymules in *Haemodorum* are interpreted as being a modification of the bifurcate cyme. A tendency for trifurcate cyme units is found only in *Dilatris* and *Lachnanthes*.

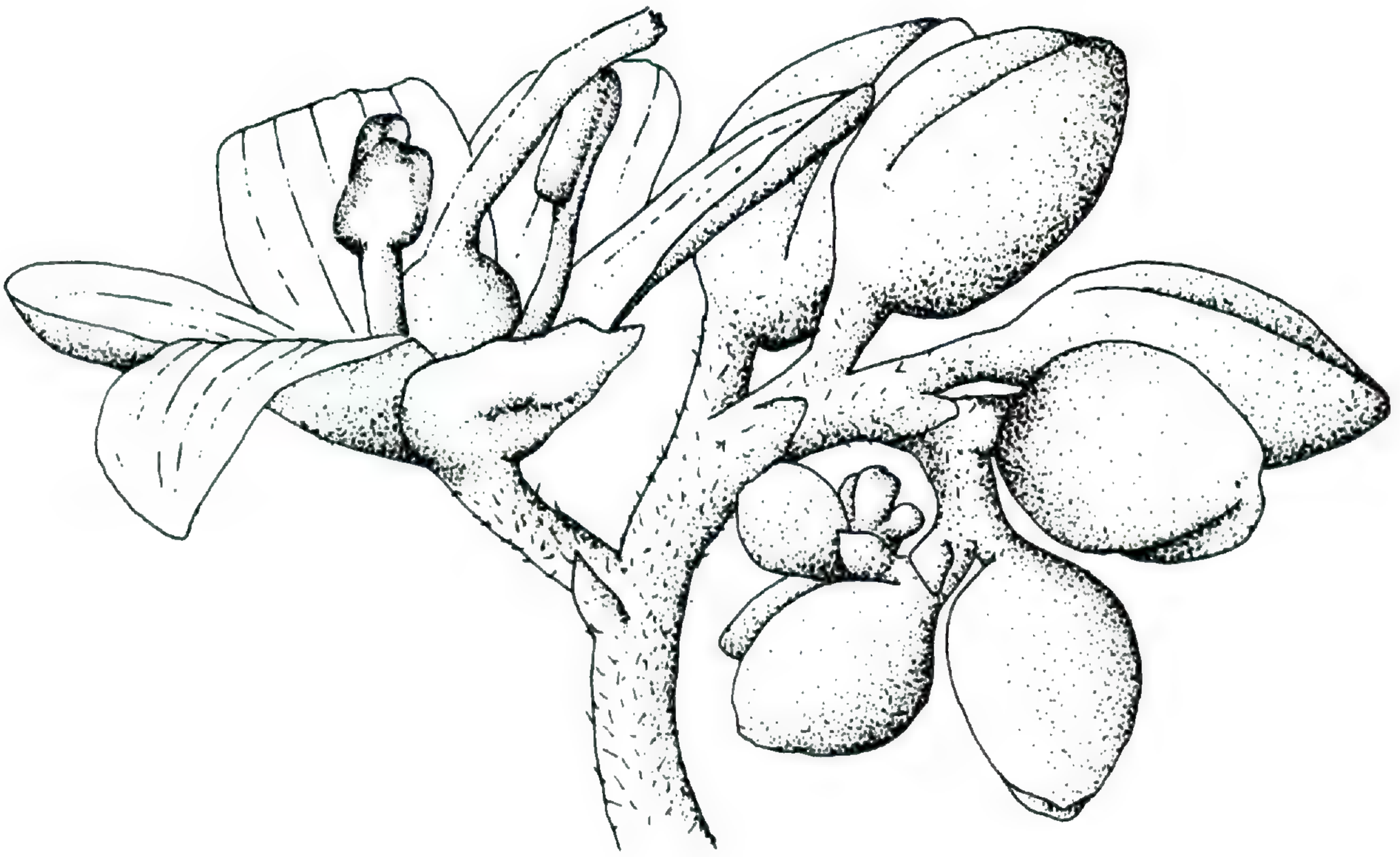
Among the outgroups all members of the Philydraceae lack cyme units; the inflorescence is either a simple spike or a spike of spikes. The inflorescence type in the Pontederiaceae is generally a spike or raceme of simple cyme units. A priori, it seems most probable that the simple cyme inflorescence unit, which is common in the monocotyledons as a whole, may be most ancestral for the Haemodoraceae; this hypothesis will be tested by the cladistic analysis.

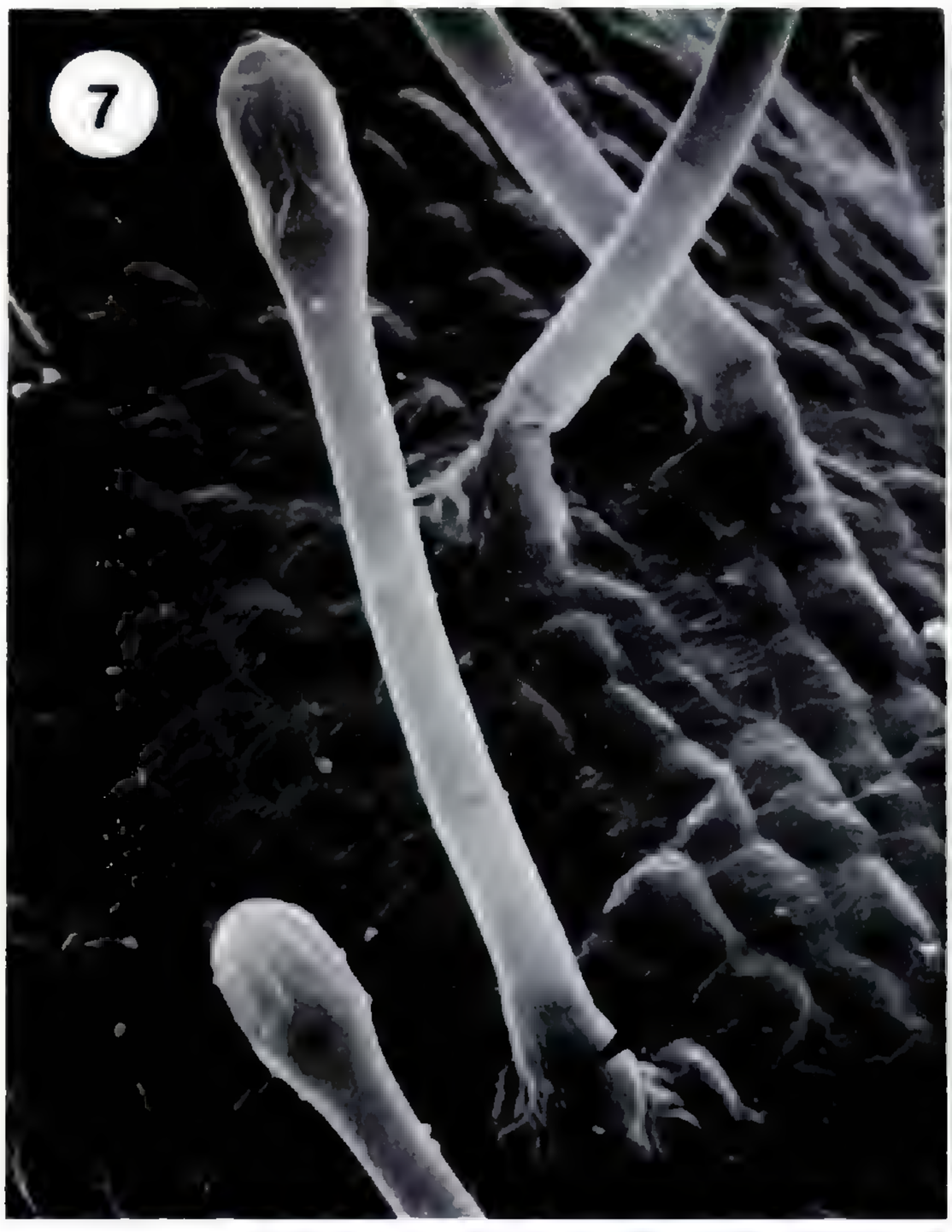
Characters #7–13. Trichome anatomy. Trichomes are present on the inflorescence axes, bracts, outer perianths, and/or ovary surfaces of all genera of the Haemodoraceae and on the leaves



FIGURES 2–5. Vegetative characters of *Wachendorfia*.—2. Cormose rootstock of *W. paniculata*; ×0.35.—3. *Wachendorfia paniculata* plant, showing plicate leaves; ×0.35.—4. Leaf of *W. thyrsiflora*. Note plication of blade; ×0.35.—5. Leaf cross section of *W. thyrsiflora*. Note plication and ridges of tissue at major vascular bundles; ×7.4.

of some family members. Distinctive pilate trichomes (Figs. 7, 9), consisting of a basal rosette of generally 3–5 cells (having characteristic transverse ridges; see Fig. 11), a uniseriate column of (1–)2–5(–7) cells, and a terminal, ovoid glandlike cell, are found in *Barberetta*, *Dilatris*, *Lachnanthes*, *Pyrrorhiza*, *Schiekia*, *Wachendorfia*, and *Xiphidium*. As their anatomical similarity reveals, the trichomes in these taxa are undoubtedly homologous. Within these seven genera various combinations with other trichome types may occur. *Barberetta* (Fig. 9) and *Xiphidium* (Fig. 20) possess only the pilate trichome type. *Pyrrorhiza* (Fig. 17), *Schiekia* (Fig. 18), and *Wachendorfia* (Fig. 19) have both pilate trichomes and sharply tapering, unicellular trichomes, both trichome types with a basal rosette of cells. *Dilatris* possesses the typical pilate trichome type (Figs. 10, 11) plus long,





FIGURES 6–8. Inflorescence and trichome morphology in the Haemodoraceae.—6. *Xiphidium coeruleum*, helicoid cyme inflorescence unit; ×7.0.—7. Pilate trichomes of *Barberetta aurea*; ×310.—8. Multiseriate, dendritic trichome of *Anigozanthos flavidus*. Note decurrent lateral trichome branches (arrow); ×470.

many-celled, uniseriate, tapering trichomes with a basal rosette of cells (Fig. 12). *Lachnanthes* has mostly long, uniseriate, tapering trichomes (Fig. 14) with *no* distinctive basal rosette (Fig. 15). However, unicellular trichomes with a glandlike terminal cell and a basal rosette of epidermal cells (resembling those of the pilate trichome type) occasionally occur on the leaf margins in *Lachnanthes* (Fig. 16).

Species of *Haemodorum* are usually glabrous throughout. However, at least *H. spicatum* (Fig. 13) has uniseriate, generally three-celled trichomes without specialized basal epidermal cells. These trichomes have a rounded, somewhat elongate terminal cell with densely brown-colored cytoplasmic contents, resembling (and possibly homologous with; see below) the terminal cell of the pilate trichome type.

Anigozanthos, *Blancoa*, *Conostylis*, and *Macropidia* have identical short to very elongate, multiseriate, highly branched, "dendritic" trichomes (Figs. 8, 21, 22). The bases of these dendritic trichomes consist of a few small, thick-walled cuboidal cells (as in Fig. 22); cells that form the branches are decurrent along the trichome axis (see Fig. 8). *Tribonanthes* has long, many-celled, generally uniseriate trichomes (Fig. 27) that are characteristically branched at the base and have 2–4 rounded to short-cylindrical basal cells (Fig. 26). One species of *Phlebocarya*, *P. pilosissima*, has branched dendritic (Fig. 24) to stellate (Fig. 25) trichomes; these are similar to but less highly branched than the dendritic trichomes of the above four genera. A second species of *Phlebocarya*, *P. ciliata*, is, like *Haemodorum*, usually glabrous but has occasional, slightly elongate, unicellular trichomes (Fig. 23) resembling those of *Haemodorum spicatum*. Thus the trichomes of *Phlebocarya* might be interpreted as a morphological and evolutionary intermediate to those of *Haemodorum* and the taxa with dendritic trichomes.

A hypothesized intergradation series for trichome anatomy in the Haemodoraceae is seen in Figure 28. Note that the homology of the trichomes of *Haemodorum* with the pilate trichome type of *Barberetta* and *Xiphidium* and with the unicellular type of *Phlebocarya* is questionable. The seven genera with pilate trichomes (having a basal rosette of epidermal cells) are arranged in a linear series depending on the presence and length of an additional trichome type, whether: (1) absent (*Barberetta*, *Xiphidium*); (2) unicellular (*Pyrrorhiza*, *Schiekia*, and *Wachendorfia*); (3) long-uniseriate (*Dilatris*); or (4) long-uniseriate lacking a basal rosette (*Lachnanthes*). The basally branched, uniseriate trichomes of *Tribonanthes* and the highly branched, dendritic trichomes of *Anigozanthos*, *Blancoa*, *Conostylis*, and *Macropidia* are depicted as intergrading with the sparsely branched dendritic trichomes of *Phlebocarya*. The long-uniseriate trichomes of *Lachnanthes* and the long-uniseriate, basally branched trichomes of *Tribonanthes* are possibly homologous; both trichome types lack a basal rosette of epidermal cells.

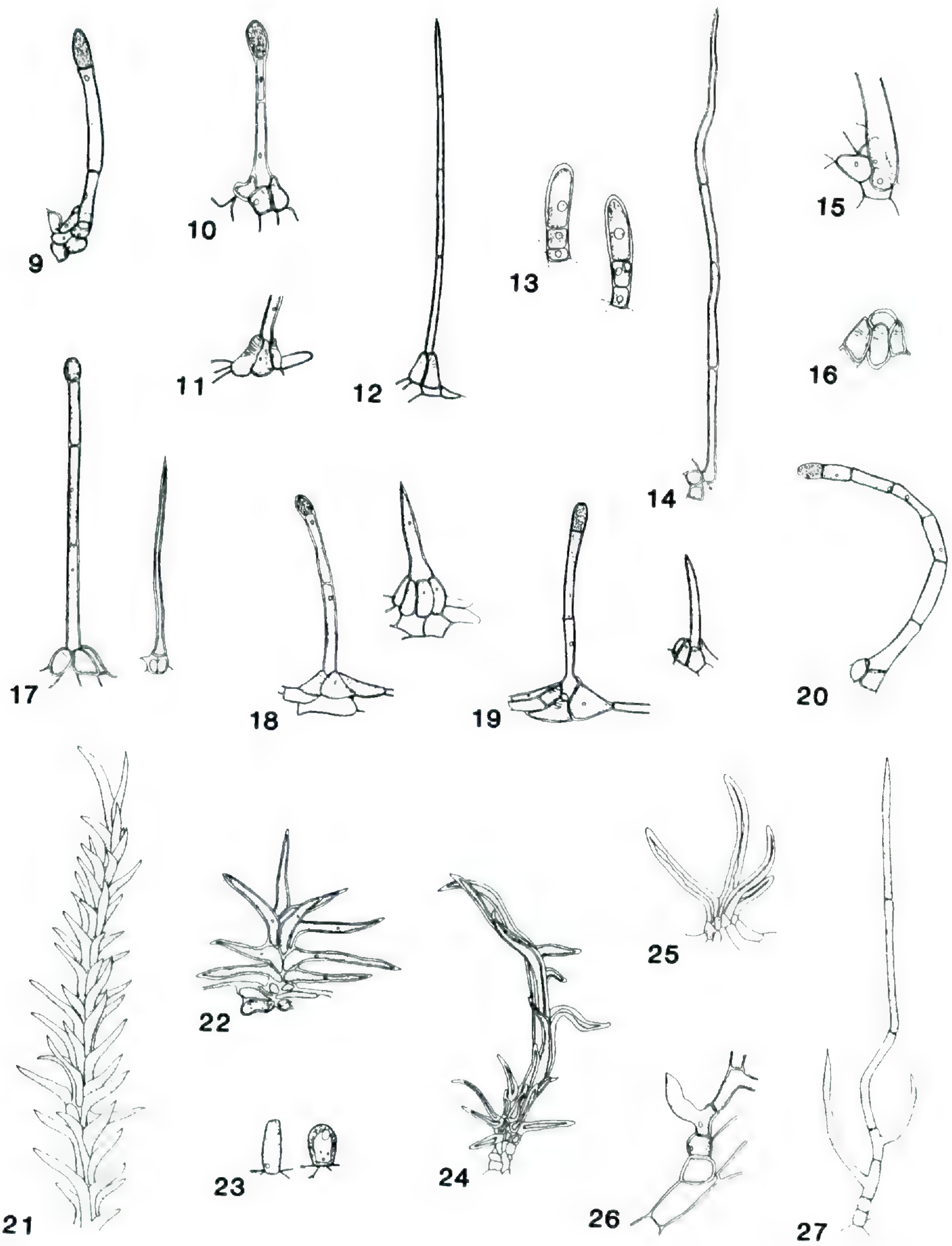
Because of the uncertainty of some of the intergrading states of Figure 28, and because the groupings of this morphocline would tend to bias the cladistic analysis if (as often happens) any conflicts in character evolution are evident, the character "trichome anatomy" was subdivided into the following discrete two-state characters (see Table 7 and Fig. 165A):

Character #7: Presence/absence of pilate trichomes. *Haemodorum*, whose trichomes are quite different than those of other taxa, is coded as possessing pilate trichomes. *Lachnanthes*, which has unicellular trichomes with a basal rosette of cells (similar to that of other taxa), is coded as "X" because of the uncertainty of homology with the pilate type. The genus *Phlebocarya*, which has unicellular trichomes in one species (*P. ciliata*), is also coded as "X" for this character so as not to bias the possibility of homology between its trichome type and that of *Haemodorum* (see Figs. 28, 165A).

Character #8: Presence/absence of trichomes which, if pilate, have a basal rosette of epidermal cells. The trichomes of *Haemodorum*, although pilate, lack this distinctive basal rosette. The unicellular trichomes of *Lachnanthes*, while coded as questionably pilate, do possess a basal rosette; thus, character #8 is coded as "present" for this species. Taxa lacking pilate trichomes are coded as "X" (including *Phlebocarya*).

Character #9: Presence/absence of trichomes with a sharply tapering apex. The basally branched trichomes of *Tribonanthes* are interpreted as being sharply tapering, as are the uniseriate trichomes of *Dilatris* and *Lachnanthes* and the unicellular trichomes of *Pyrrorhiza*, *Schiekia*, and *Wachendorfia*. Taxa with multiseriate, dendritic trichomes were also coded as possessing tapering trichomes because of the presumed homology of the sharply tapering trichome branches with the sharply tapering apices of the uniseriate trichomes.

Character #10: Trichomes which, if tapering, are either unicellular (*Pyrrorhiza*, *Schiekia*, and *Wachendorfia*) or multicellular. Taxa lacking tri-



FIGURES 9–27. Trichome anatomy in the Haemodoraceae.—9. *Barberetta aurea*, pilate trichome. Note terminal granular cell and basal rosette of cells; ×120. 10–12. *Dilatris pilansii*.—10. Pilate trichome; ×120.—11. Basal rosette cells with apical transverse ridges; ×73.—12. Long, uniseriate tapering trichome with basal rosette cells; ×54.—13. *Haemodorum spicatum*, short, uniseriate (generally 3-celled) trichome. Note oblong, granular terminal cell; ×133. 14–16. *Lachnanthes caroliniana*.—14. Long, uniseriate tapering trichome; ×55.—15. Close-up of trichome base. Note absence of rosette cells; ×120.—16. Unicellular trichome of leaf margins. Note basal rosette cells with transverse ridges; ×146.—17. *Pyrrorhiza neblinae*, pilate (left) and unicellular, sharply tapering (right) trichomes, both with basal rosette cells; ×51 (left), ×40 (right).—18. *Schiekia orinocensis*, pilate (left) and unicellular, sharply tapering (right) trichomes; ×73.—19. *Wachendorfia thyrsiflora*, pilate (left) and unicellular, sharply tapering (right) trichomes; ×73.—20. *Xiphidium coeruleum*, pilate trichome with basal rosette cells; ×120. 21, 22. *Anigozanthos flavidus*.—21. Long, dendritic trichome with decurrent lateral branches; ×40.—22. Short, dendritic trichome with small cuboidal basal cells; ×69.—23. *Phlebocarya ciliata*, unicellular trichomes with granular contents; ×67. 24, 25. *Phlebocarya pilosissima*.—24. Dendritic trichome, with decurrent lateral branches and cuboidal basal cells; ×73.—25. Stellate trichome; ×91. 26, 27. *Tribonanthes variabilis*.—26. Trichome base, showing cuboidal basal cells and basal, lateral branches; ×120.—27. Uniseriate, tapering, basally brached trichome; ×50.

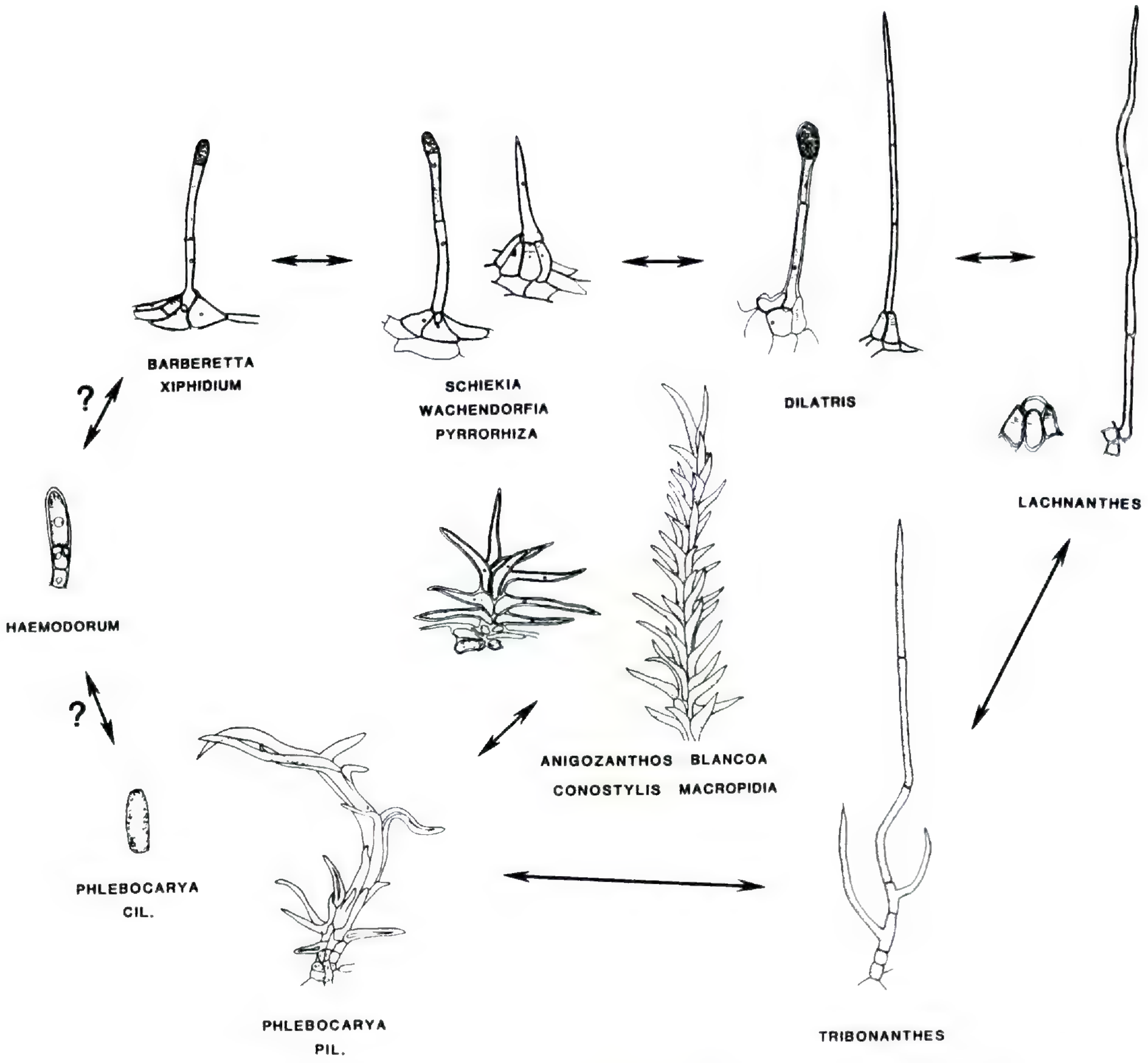


FIGURE 28. Hypothesized intergradation series of trichome types in the Haemodoraceae. Note the uncertainty (indicated by "?") of homology of the trichomes of *Haemodorum*. (See text for character state coding.)

chomes with sharply tapering apices are coded as "X."

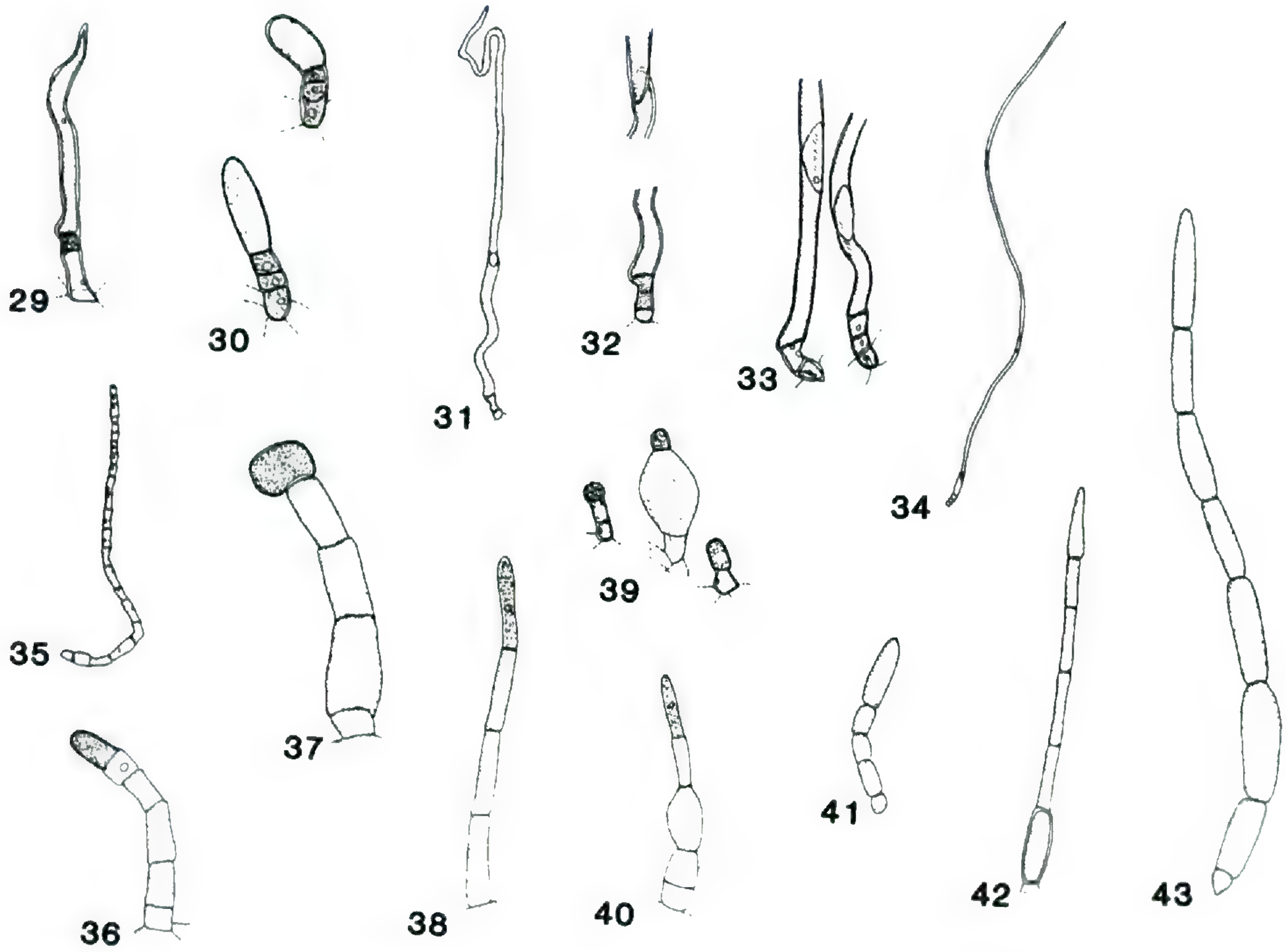
Character #11: Trichomes which, if tapering, are either uniseriate or multiseriate, the latter also being dendritic with decurrent branches and with multiseriate cuboidal basal cells. Taxa lacking tapering trichomes are coded as "X."

Character #12: Trichomes which, if tapering, are unbranched vs. branched. Branched trichomes include both the multiseriate, dendritic trichomes and the basally branched trichomes of *Tribonanthes*. Taxa lacking tapering trichomes are coded as "X."

Character #13: Presence/absence of trichomes which, if tapering, possess a basal rosette of epidermal cells. *Lachnanthes*, *Tribonanthes*, and the multiseriate taxa are coded as lacking the basal rosette (in the tapering trichomes) possessed by *Dilatris*, *Pyrrorhiza*, *Schiekia*, and *Wachendorfia*. Taxa lacking tapering trichomes are coded as "X."

For character #9 it might be argued that taxa with dendritic trichomes should not be coded as "tapering"; i.e., the sharply tapering branches of these multiseriate trichomes may not be homologous with the sharply tapering apices of the uniseriate trichomes. However, if taxa with multiseriate trichomes (*Anigozanthos*, *Blancoa*, *Conostylis*, *Macropidia*, and *Phlebocarya*) are coded as either "0" or as "X" for this character, the topology of the most parsimonious cladogram(s) is unaffected (see Cladistic Analysis).

Trichomes of the outgroup families show some resemblances to those of the Haemodoraceae. For



FIGURES 29–43. Trichome anatomy in the Philydraceae and Pontederiaceae. 29–32. *Helmholtzia acorifolia*. —29. Three-celled, uniseriate trichome, middle cell cuboidal with granular contents; ×117.—30. Four-celled, pilate trichomes, the terminal cell with orange-brown contents; ×146.—31. Long, uniseriate, tapering trichome; note short basal cells; ×52.—32. Close-up of trichome illustrated in Figure 31, showing oblique cross-walls at junction of cells (above) and trichome base with short, basal cells (below); ×117. 33–34. *Philydrum lanuginosum*.—33. Trichome bases. Note oblique cross-walls and cuboidal basal cells; ×117.—34. Long, uniseriate, tapering trichome; ×40. 35–37. *Heteranthera reniformis*.—35. Uniseriate, many-celled trichome of stamen filament; ×40.—36. Short, uniseriate pilate trichome of style; note granular contents of terminal cell; ×146.—37. Pilate trichome of outer tepal surface. Note granular contents of terminal cell; ×106. 38–40. *Pontederia cordata*.—38. Four-celled uniseriate trichome. Note granular contents of terminal cell; ×51.—39. Two- or three-celled trichomes. Note small terminal cell with granular contents and (in middle trichome) enlarged subapical cell containing orange-brown ergastic substance; ×73.—40. Five-celled uniseriate trichome, having granular contents in terminal cell and orange-brown ergastic substance in middle cell; ×51. 41–43. *Reussia rotundifolia*.—41. Five-celled, uniseriate trichome; ×39.—42. Six-celled, uniseriate trichome, with granular contents in supra-basal cell; ×39.—43. Eight-celled, uniseriate trichome; ×39.

example, *Helmholtzia* (Figs. 29, 31, 32) and *Philydrum* (Figs. 33, 34) of the Philydraceae have elongate, uniseriate, tapering trichomes with two or three isodiametric basal cells and, in the more distal regions, steeply inclined, overlapping end walls (see Figs. 32, 33). These trichomes most resemble *Tribonanthes*, which, however, are basally branched and have transverse, not inclined, end walls. *Helmholtzia* possesses, in addition to the above trichome type, occasional three- to four-celled, pilate trichomes (Fig. 30) with an ovoid to slightly elongate terminal cell containing a clear orange-brown ergastic substance similar to that found in perianth idioblasts in this and other genera (see *Perianth tannin cells/idioblasts*). These trichomes show some resemblance to the pilate trichomes of the Haemodoraceae, differing primarily in the contents and appearance of the terminal cell and in lacking the distinctive basal rosette of epidermal cells. Within the investigated members of the Pontederiaceae, the genus *Heteranthera* is largely glabrous but has some floral trichomes; these include: (1) multicellular, uniseriate staminal filament trichomes (Fig. 35); (2) short, pilate stylar trichomes with a terminal cell containing granular contents (Fig. 36); and (3) larger pilate trichomes, located on the outer tepal surfaces, with a globose terminal cell containing granular contents (Fig. 37). The so-called pilate trichomes of *Heteranthera* resemble somewhat the pilate trichomes in the Haemodoraceae, but (as in *Helmholtzia*) they lack the distinctive basal rosette cells. The one investigated species of *Pontederia* has several different, intergrading trichome types, ranging from: (1) linear,

uniseriate, 3–6-celled, with a densely granular terminal cell (Fig. 38); (2) short, 2–3-celled and capitate with a spherical to ellipsoid terminal cell (Fig. 39); and (3) uniseriate, of variable length, with one or more cells enlarged and containing a clear, orange ergastic substance similar to that in *Helmholtzia* (Fig. 40). The pilate trichomes of *Pontederia* are like those in *Helmholtzia* of the Philydraceae and show some resemblance to the pilate trichomes in the Haemodoraceae. *Reussia* of the Pontederiaceae has several types of uniseriate perianth trichomes (Figs. 41–43), some of which have a terminal cell containing densely granular contents.

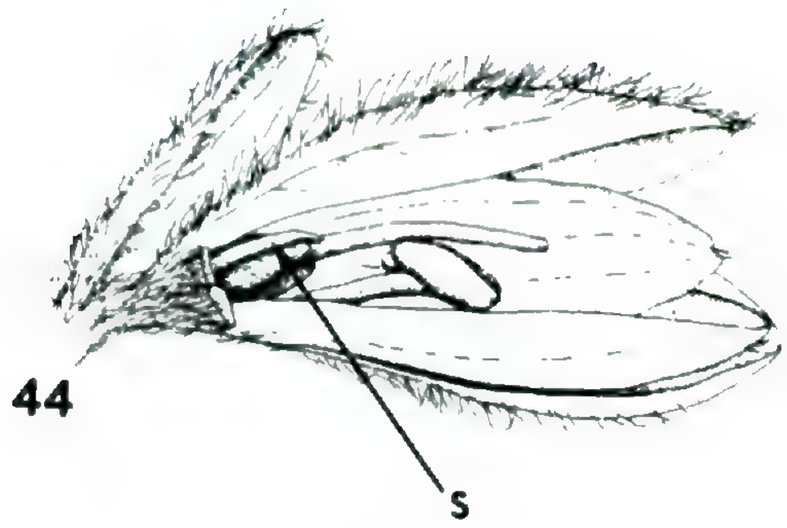
Many similarities are seen between the Haemodoraceae and the outgroups with respect to trichome anatomy. In the present analysis if one or more outgroup(s) possessed a trichome type similar to that designated in the character analysis, then that feature was coded as being homologous with the condition found in the Haemodoraceae. It is thus hypothesized that the similarity of the pilate trichomes of *Heteranthera* (Pontederiaceae) or the uniseriate trichomes of *Helmholtzia* (Philydraceae), as examples, with members of the Haemodoraceae reflects common ancestry. A possible difficulty with this, however, is that both outgroups are polymorphic with regard to trichome type. However, when the two were coded as polymorphic ("?") for all trichome characters (characters #7–13) in a separate cladistic analysis, the topology of the resultant most parsimonious cladograms remains unchanged (see Cladistic Analysis).

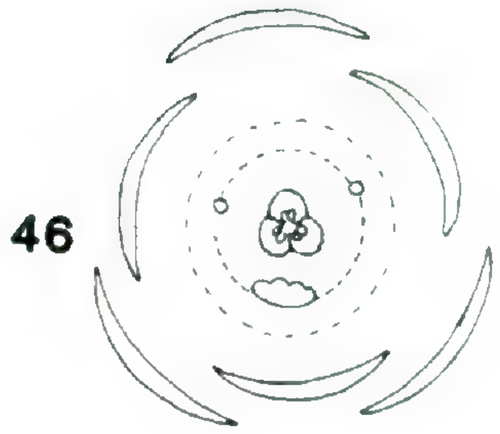
Character #14. Perianth apertures. *Schiekia* (Fig. 47) and *Wachendorfia* (Fig. 51) are similar in that the outer posterior tepal is basally fused to the two outer latero-anterior tepals and to the two inner latero-posterior tepals (Figs. 50, 52). At the basal junctions between the two outer latero-anterior tepals and the outer posterior tepal are distinctive slitlike pouches (termed "apertures" for *Wachendorfia* by Ornduff & Dulberger, 1978). Ornduff & Dulberger reported that in *Wachendorfia paniculata* nectar is produced from these perianth apertures. However, in view of the presence of septal nectaries in *Wachendorfia* species (see *Septal nectaries*), it is probable that these apertures function solely as a collection site for nectar secreted from the ovary. The significance of these sites is unknown, as no insect or other visitors have been described for *Wachendorfia*. The perianth apertures in *Schiekia* probably function similarly to those in *Wachendorfia*, although no observations have been published. All other genera of the Haemodoraceae with basically distinct tepals have no basal fusion of the tepals and no perianth apertures. Many genera of the Haemodoraceae have a syntepalous perianth, but fusion in these taxa is in the form of a complete basal perianth tube (see *Perianth tube*) and is treated as nonhomologous with the rather unique tepallary fusion in *Schiekia* and *Wachendorfia*.

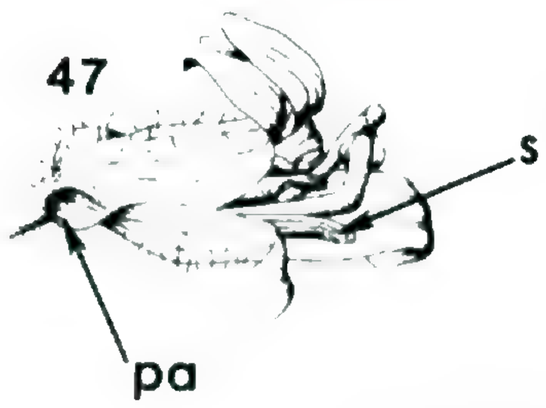
Among the outgroup taxa, all members of the Philydraceae have a four-parted perianth, the upper component consisting of the fusion product of the inner posterior and outer latero-posterior tepals (Hamann, 1966). Members of the Pontederiaceae possess six imbricate tepals variously fused into a basal tube; in some taxa (e.g., *Pontederia*) lateral and anterior open slits are present at the base of the perianth tube. However, neither outgroup has the distinctive perianth apertures seen in *Schiekia* and *Wachendorfia* and are coded as lacking this feature.

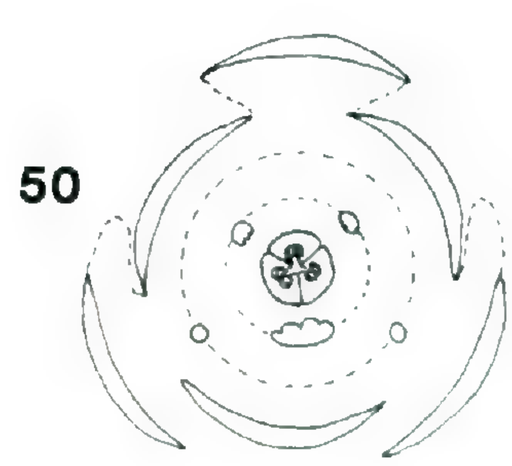
Characters #15, 16. Perianth tube. A basal perianth tube is possessed by five genera in the Haemodoraceae: *Anigozanthos* (Figs. 53, 54), *Blancoa* (Fig. 55), *Conostylis* (Fig. 56), *Macropidia* (Fig. 57), and *Tribonanthes* (Fig. 58). (*Conostylis breviscapa* lacks a perianth tube and has distinct tepals. In view of the numerous (ca. 24) species of *Conostylis* that possess a perianth tube, the distinct tepals of *C. breviscapa* are tentatively hypothesized to have evolved secondarily from an ancestral perianth tube; this matter needs further investigation.) All other members of the family, including *Phlebocarya* (Fig. 60), lack a complete perianth tube. As discussed under *Perianth apertures*, the unique tepallary fusion in *Schiekia* and *Wachendorfia* is coded as nonhomologous with the tubular perianth of the above genera and is treated as a separate character. Of the taxa with perianth tubes, *Anigozanthos*, *Blancoa*, *Conostylis androstemma*, *C. bealiana*, and *Macropidia* have a very elongate perianth tube (Figs. 53–55, 57). The evolution of an elongate perianth tube in at least *Anigozanthos*, *Blancoa*, and *Macropidia* is almost certainly correlated with selective pressure for bird pollination (Hopper, 1977; Hopper & Burbidge, 1978; Keighery, 1981). Therefore, presence of an elongate perianth tube is designated as derived from an ancestor with a short perianth tube: PERIANTH TUBE ABSENT ←[#15]→ SHORT PERIANTH TUBE ←[#16]→ LONG PERIANTH TUBE.

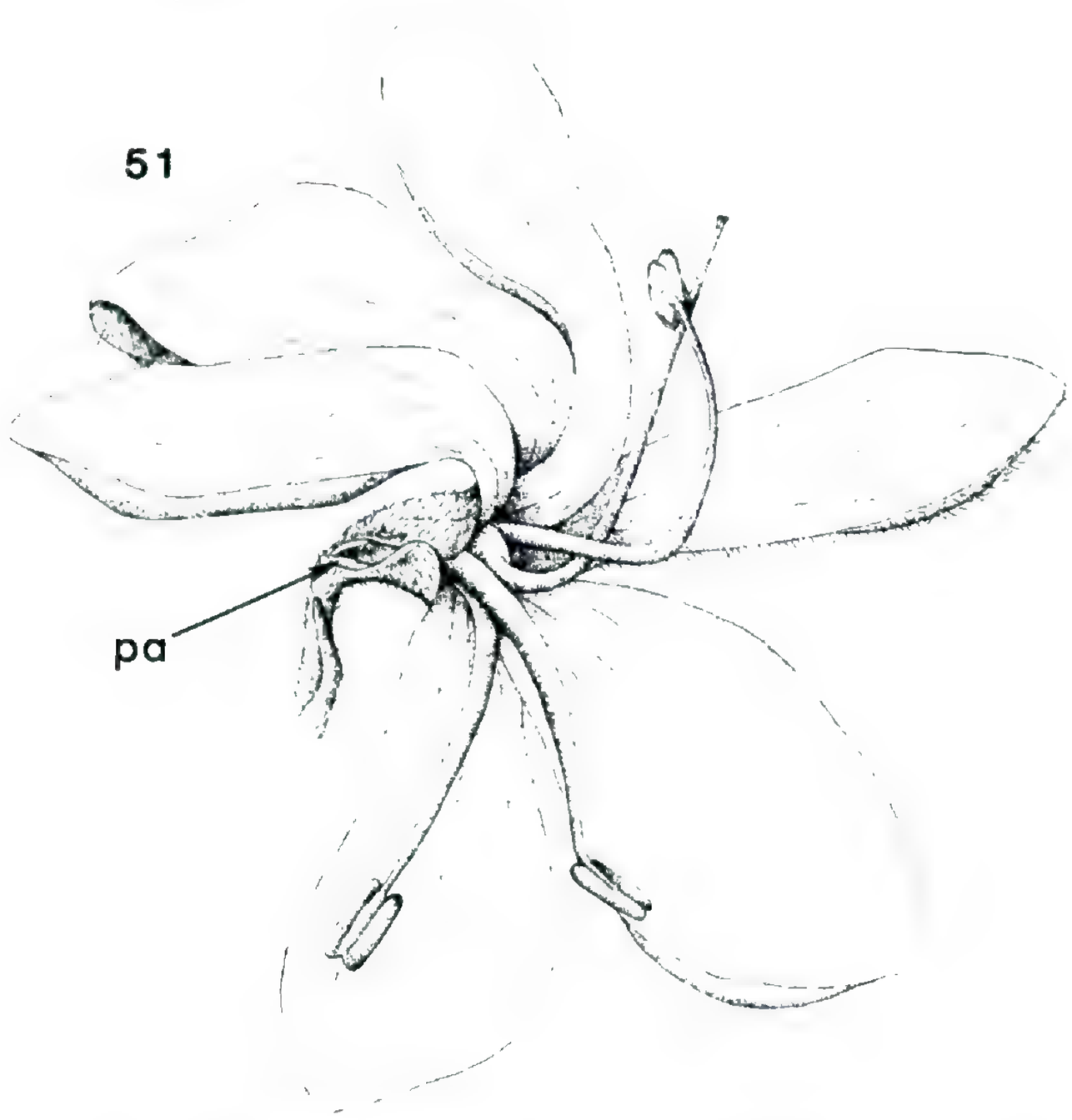
As discussed above (see *Perianth apertures*), the outgroup taxa have some variation of perianth fusion. All members of the Philydraceae have a

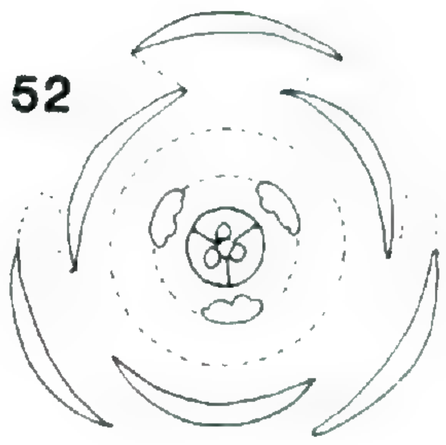








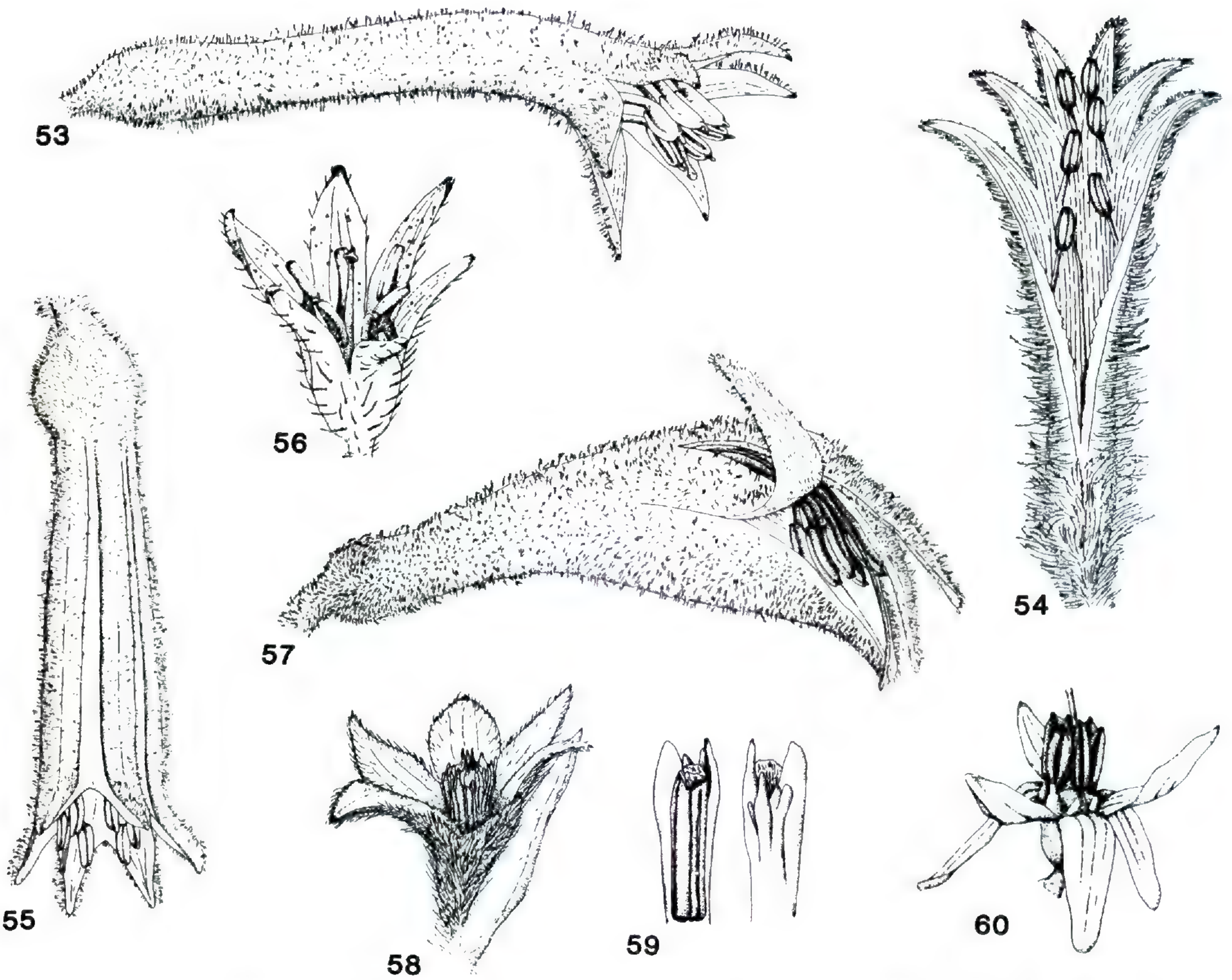




FIGURES 44–52. Floral morphology in the Haemodoraceae. 44–46. *Pyrrorhiza neblinae*.—44. Whole flower, two tepals removed, showing one of two staminodes (s) and single stamen; ×2.8.—45. Adaxial view of staminode; ×5.7.—46. Floral diagram. 47–50. *Schiekia orinocensis*.—47. Whole flower. Note perianth aperture (pa) and one of two staminodes (s); ×3.6.—48. Staminode, adaxial view; ×5.7.—49. One of two latero-posterior stamens. Note small (caducous) anther with basal constriction.—50. Floral diagram. 51, 52. *Wachendorfia paniculata*.—51. Whole flower. Note perianth aperture (pa); ×2.8.—52. Floral diagram.

rather specialized four-parted perianth, the upper component consisting of the fusion product of the inner posterior and outer latero-posterior tepals. Because tepallary fusion in the Philydraceae is incomplete and rather specialized, it is coded non-homologous with the short or long perianth tube of the Haemodoraceae, which results from fusion of all six tepals. Members of the Pontederiaceae possess six imbricate tepals which vary from essentially distinct to being connate and forming a short or long perianth tube; thus, the Pontederiaceae are coded as polymorphic for both characters.

Character #17. Perianth symmetry. *Pyrrorhiza* (Fig. 44), *Schiekia* (Fig. 47), and *Wachendorfia* (Fig. 51) have zygomorphic perianths. All other family members have basically actinomorphic perianths, with the exception of *Anigozanthos* and *Macropidia*, in which zygomorphy is thought to have been derived independently (see *Perianth splitting*).



FIGURES 53–60. Floral morphology in the Haemodoraceae. 53, 54. *Anigozanthos*.—53. *A. flavidus*; ×1.4.—54. *A. humilis*; ×1.35.—55. *Blancoa canescens*; ×3.0.—56. *Conostylis aurea*; ×3.5.—57. *Macropidia fuliginosa*; ×2.4. 58–59. *Tribonanthes variabilis*.—58. Whole flower; ×2.4.—59. Stamen, adaxial (left) and abaxial (right) views. Note connective appendages; ×2.0.—60. *Phlebocarya ciliata*; ×3.75.

Among the outgroups, all species of the Philydraceae have zygomorphic perianths. However, because this family possesses a rather specialized perianth consisting of fusion of the posterior tepals and reduction of the latero-anterior tepals, perianth symmetry in the Philydraceae is coded as having uncertain homology ("?") with that in the Haemodoraceae. In the Pontederiaceae perianth symmetry is either actinomorphic or more rarely zygomorphic and is coded as polymorphic ("?").

Among angiosperms as a whole, zygomorphy is generally considered to be a derived feature, usually correlated with specialized pollination systems (Faegri & van der Pijl, 1966; Sporne, 1975). The relative ancestry of this feature and its significance in pollination mechanisms in the Haemodoraceae will be discussed with reference to the cladistic analysis.

Character #18. Perianth splitting. Two other family genera, *Anigozanthos* (Figs. 53, 54) and *Macropidia* (Fig. 57), also have zygomorphic perianths. However, the perianths of these taxa are syntepalous and tubular, not basically apotepalous as in the zygomorphic *Pyrrorhiza*, *Schiekia*, and *Wachendorfia*. More importantly, zygomorphy in *Anigozanthos* and *Macropidia* arises primarily by the longitudinal "splitting" of the tube along an anterior line (Fig. 54). Zygomorphy in these two genera almost certainly has evolved independently from (and is not homologous to) that in *Pyrrorhiza*, *Schiekia*, and *Wachendorfia* and is treated as a separate character.

Among the outgroups and monocots as a whole, such perianth splitting is absent. It is extremely likely that zygomorphy in *Anigozanthos* and *Macropidia* was derived from an ancestral tubular, actinomorphic condition, as occurs in *Blancoa*. This hypothesis is supported by the fact that all three of these genera have identical valvate perianths during the early bud stage (see below). Zygomorphy in *Anigozanthos* and *Macropidia* prob-

ably evolved due to strong selective pressure for specialized bird pollination (Hopper & Campbell, 1977; Hopper & Burbidge, 1978).

Character #19. Perianth aestivation. *Anigozanthos*, *Blancoa*, *Conostylis*, *Macropidia*, and *Tribonanthes* possess a valvate perianth at anthesis, in which the perianth lobes of the mature flower show no evidence of overlap (Figs. 53–58, 62). In *Anigozanthos*, *Blancoa*, and *Macropidia* the perianth lobes are valvate even during the earliest bud developmental stage (Fig. 61). However, *Conostylis* species (Fig. 63) and *Tribonanthes* (Fig. 64) clearly have an imbricate perianth aestivation in the bud stage; only when the flowers open are the tepals valvate. In all other genera of the Haemodoraceae, tepals are imbricate throughout floral development.

An imbricate perianth, or evidence of such in cases of fusion, occurs in all species among the outgroups. It seems very likely then that the valvate perianth of the above five genera is a derived feature. The apparent developmentally valvate perianth of *Anigozanthos*, *Blancoa*, and *Macropidia* may represent a further specialization, one probably correlated with the long perianth tube in these taxa (see *Perianth tube*). Because other species of *Conostylis* having elongate perianth tubes have not been studied for this feature, possession of a valvate perianth throughout floral development is not coded separately from a valvate perianth present only at flower anthesis.

Character #20. Perianth tannin cells. Distinctive perianth idioblast cells are present in *Haemodorum*, *Phlebocarya*, and *Tribonanthes* (Figs. 65–67). These perianth idioblasts vary in length (1.5–6 times longer than broad), are oriented parallel to the tepal axis in the subepidermal layer, and are completely filled (presumably the vacuoles) with an orange to red-brown ergastic substance. The cells are scattered in the tepal among the more predominant clear parenchymatous cells. The ergastic substance looks like oil; yet staining reaction for fats and oils with Sudan IV (Johansen, 1940) was negative. Safranin red positively stains these contents, indicating the possible presence of tannins. The idioblasts are located throughout the perianth and occasionally in the ovary wall and placentae. Among all investigated members of the Haemodoraceae, perianth idioblasts are not present in the following genera: *Anigozanthos*, *Barberetta*, *Blancoa*, *Conostylis*, *Dilatris* (two species), *Lachnanthes*, *Macropidia*, *Pyrrorhiza*, *Schiekia*, *Wachendorfia* (two species), and *Xiphidium*. All of the former taxa possess only clear, generally rectangular parenchyma cells comprising the nonvascularized tissue of the perianth (illustrated for *Wachendorfia* in Fig. 70). (Incidentally, raphide sacs are present in the tepals of all investigated members of the Haemodoraceae and both outgroups.)

Among the outgroup families, perianth tannin cells virtually identical to those in *Haemodorum*, *Phlebocarya*, and *Tribonanthes* are present in all genera of the Philydraceae (Fig. 68) and in all investigated genera of the Pontederiaceae (Fig. 69), except for *Heteranthera*. Because of the great anatomical similarity between the perianth idioblasts of the outgroups and those found in the Haemodoraceae, it seems highly probable that they are homologous structures and are so coded. The absence of these perianth idioblasts in *Heteranthera* is tentatively hypothesized to be a secondary derivation within the Pontederiaceae.

Characters #21, 22. Stamen number. The number of fertile stamens per flower in taxa of the Haemodoraceae is either six, three, or one. *Schiekia* has three fertile stamens, the anterior one of which is considerably larger than the other two, plus two staminodes (Fig. 48) positioned lateroanteriorly in a whorl outer to the fertile stamens (Fig. 50). Because the two staminodes of *Schiekia* may represent vestiges (or evolutionary precursors) of an outer stamen whorl, the androecium of *Schiekia* is coded as evolutionarily intermediate between six stamens per flower and three or one stamen(s) per flower. *Pyrrorhiza* has only one fertile stamen, plus two staminodes (Fig. 45) morphologically similar to those in *Schiekia* but differing by being in the same whorl as the single

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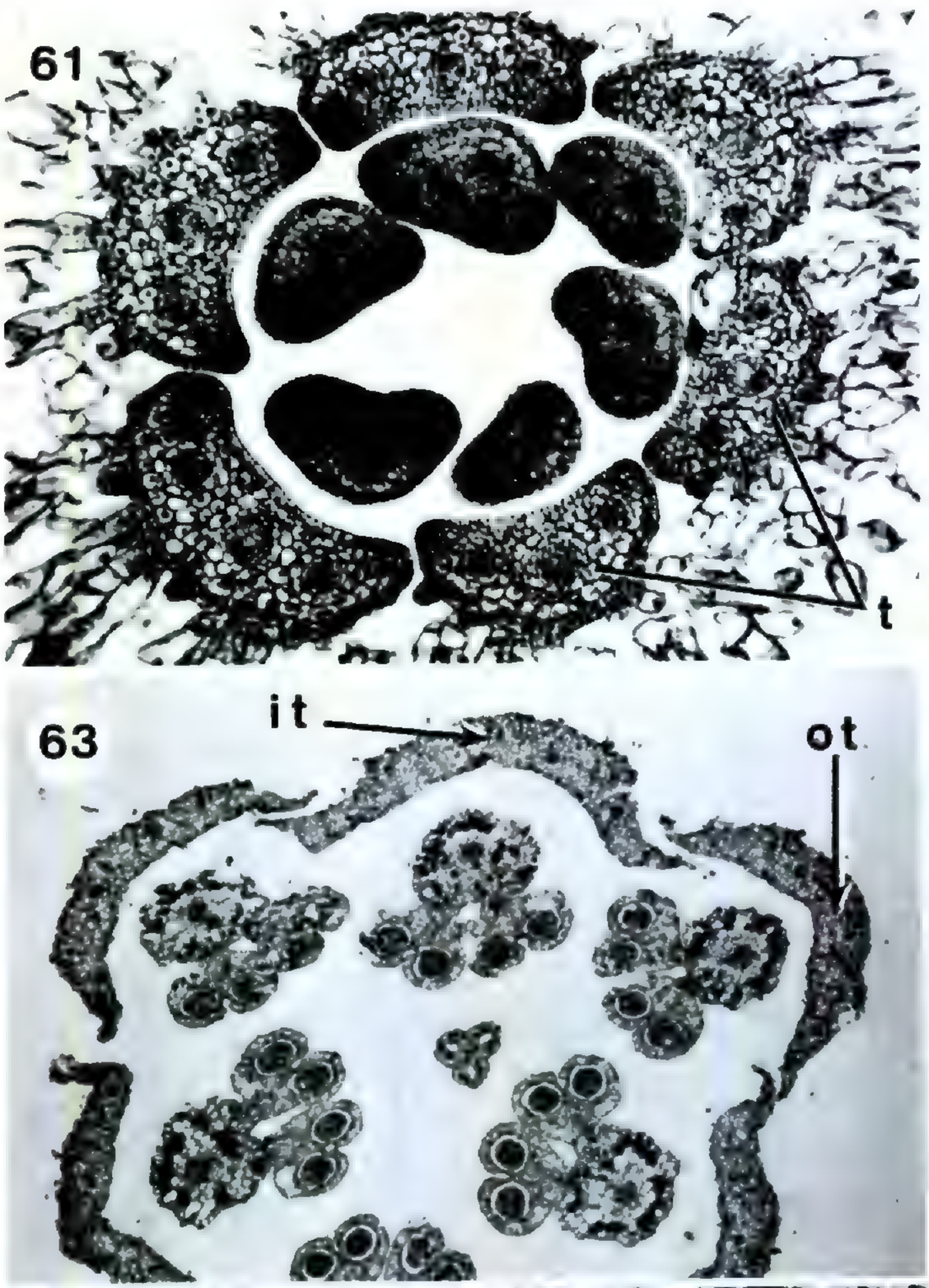
FIGURES 61–70. 61–64. Perianth aestivation. 61, 62. *Anigozanthos flavidus*.—61. Immature bud cross section. Note valvate arrangement of tepals (t); ×86.—62. Mature bud cross section. Tepals (t) remain valvately arranged; ×30.—63. *Conostylis priesii*. Mature bud cross section. Note imbricate aestivation, with outer tepal whorl (ot) overlapping inner tepal whorl (it); ×14.—64. *Tribonanthes variabilis*. Bud cross section, intermediate stage. Note outer tepal (ot) overlapping inner tepals (it); ×26. 65–69. Perianth tannin idioblast cells (id).—65. *Haemodorum spicatum*; ×200.—66. *Phlebocarya pilosissima*; ×194.—67. *Tribonanthes variabilis*; ×200.—68. *Helmholtzia acorifolia*; ×194.—69. *Pontederia cordata*; ×164.—70. Perianth cells of *Wachendorfia thyrsiflora*, which lack tanniniferous idioblasts; ×164.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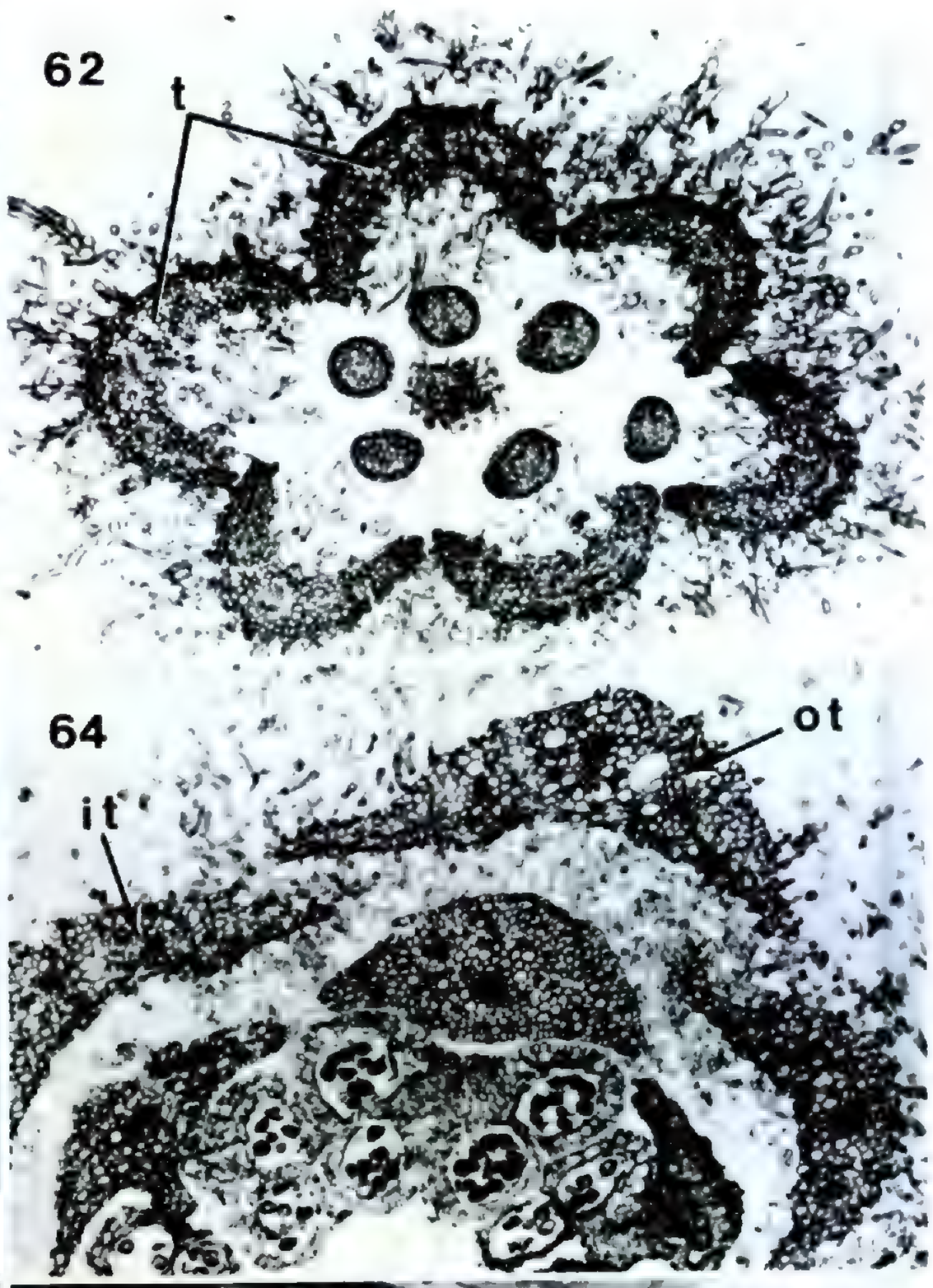
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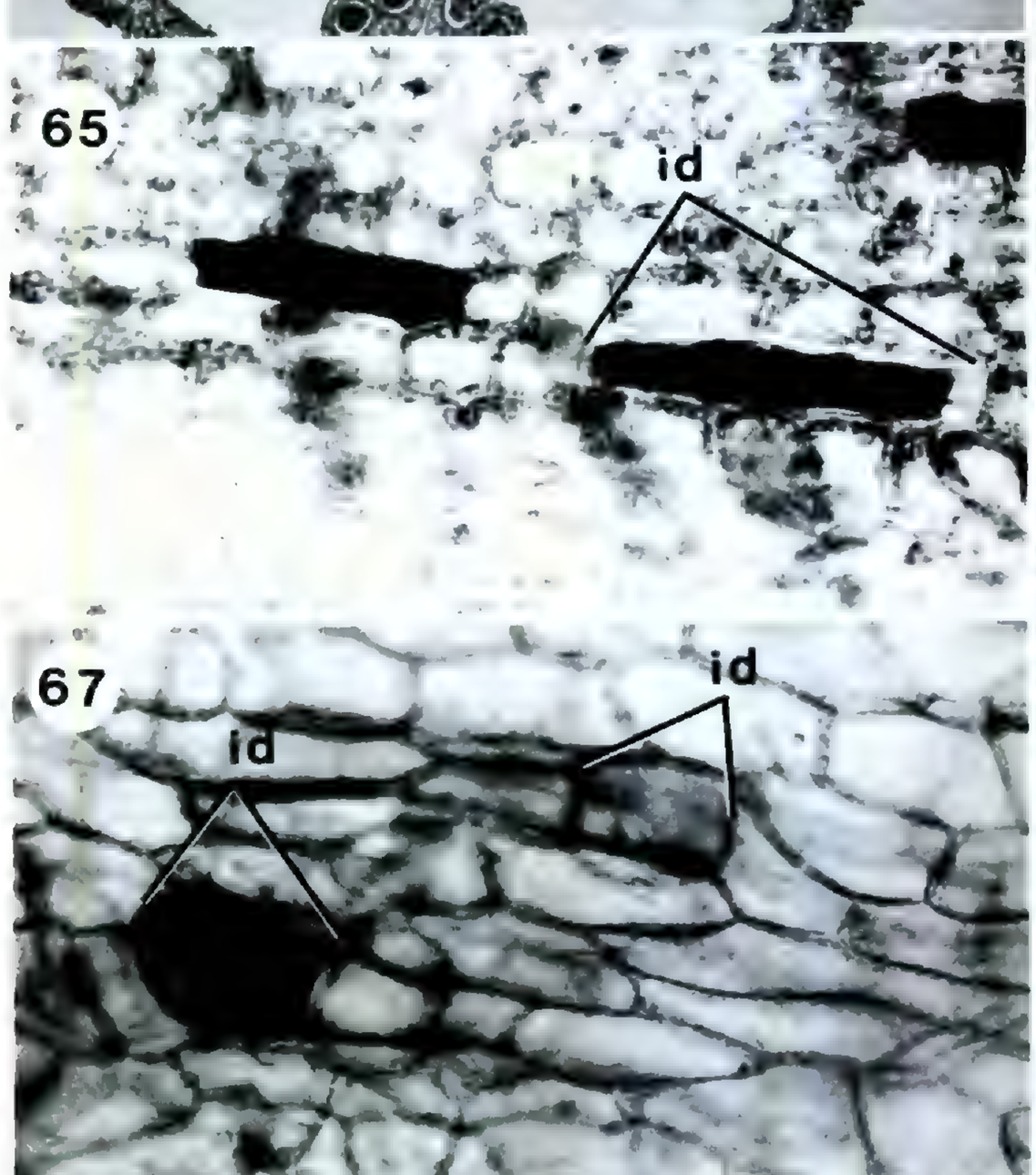
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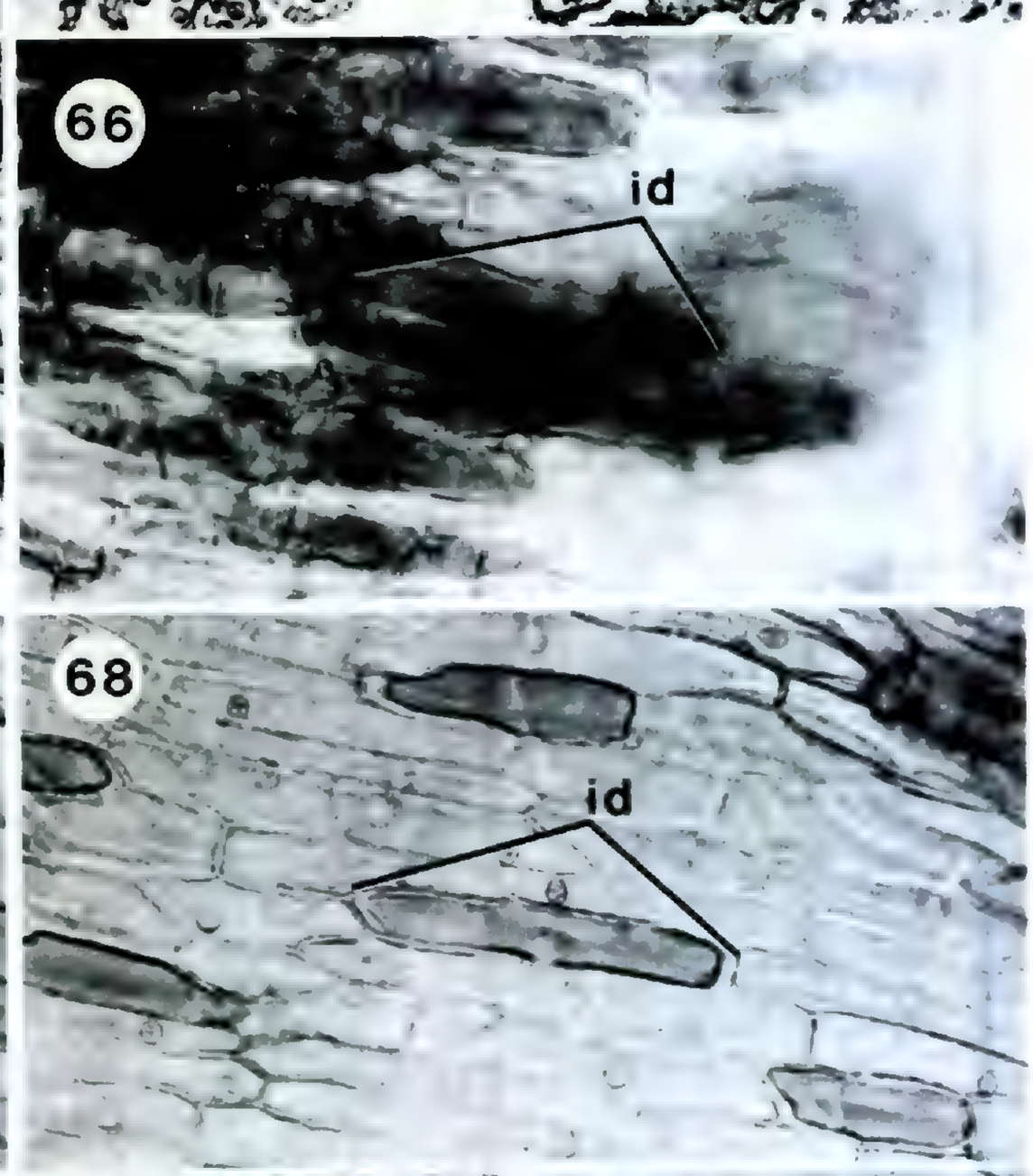
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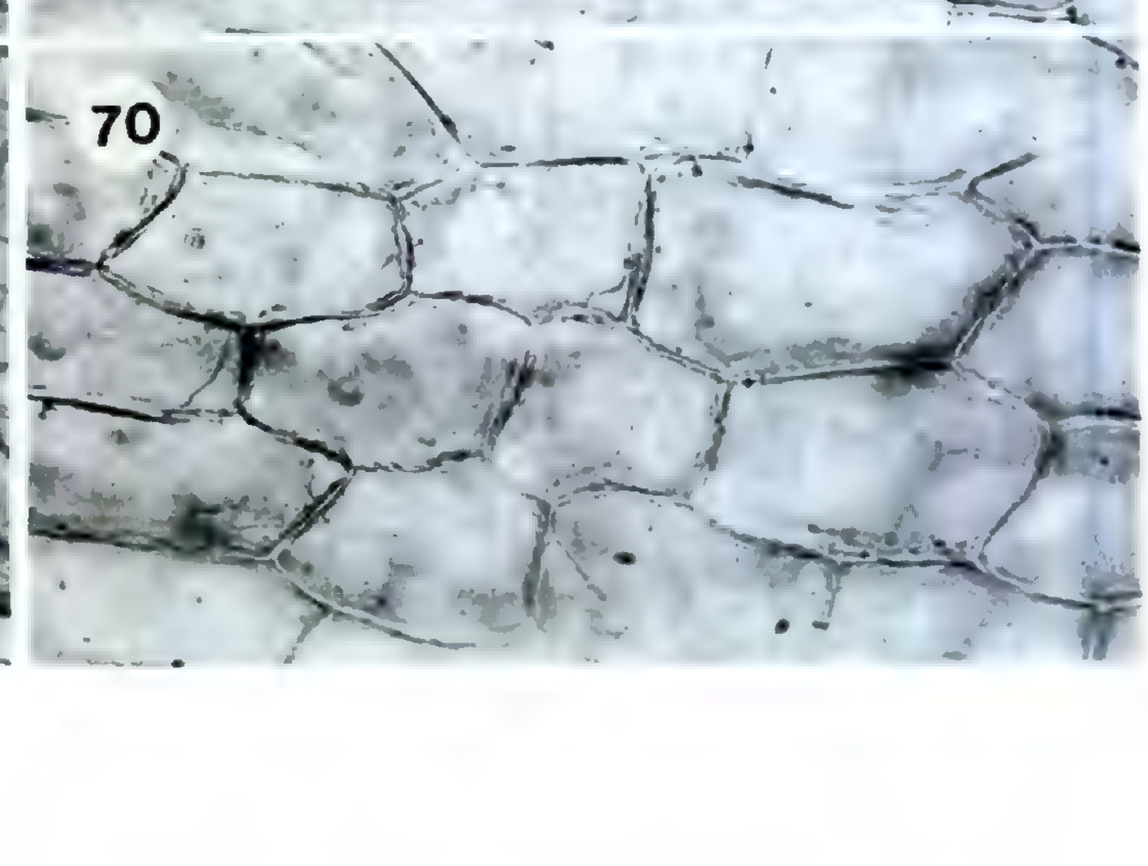
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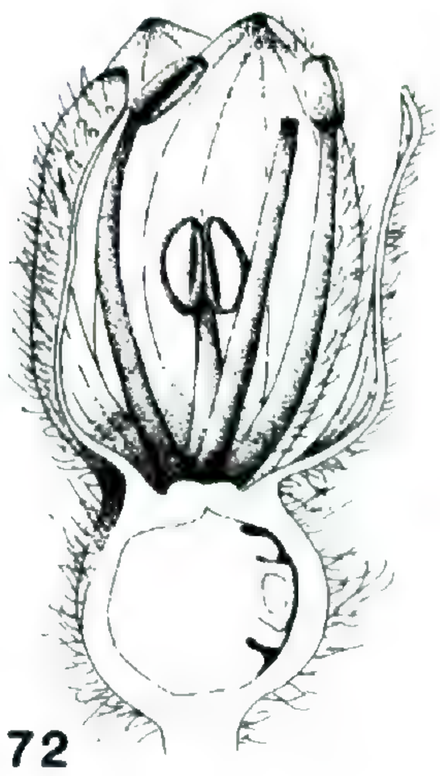
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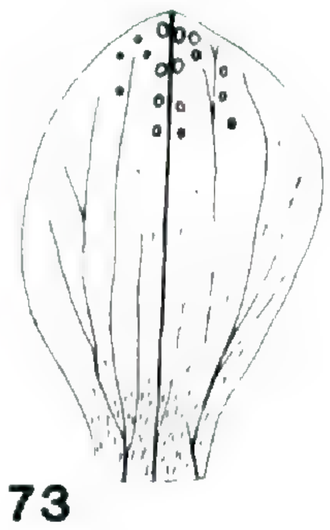
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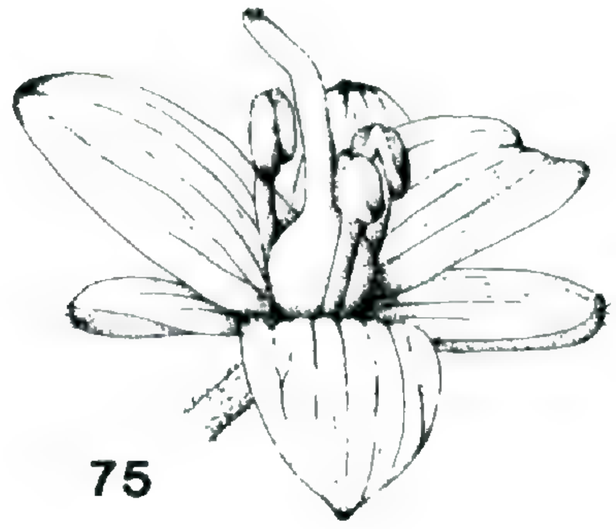
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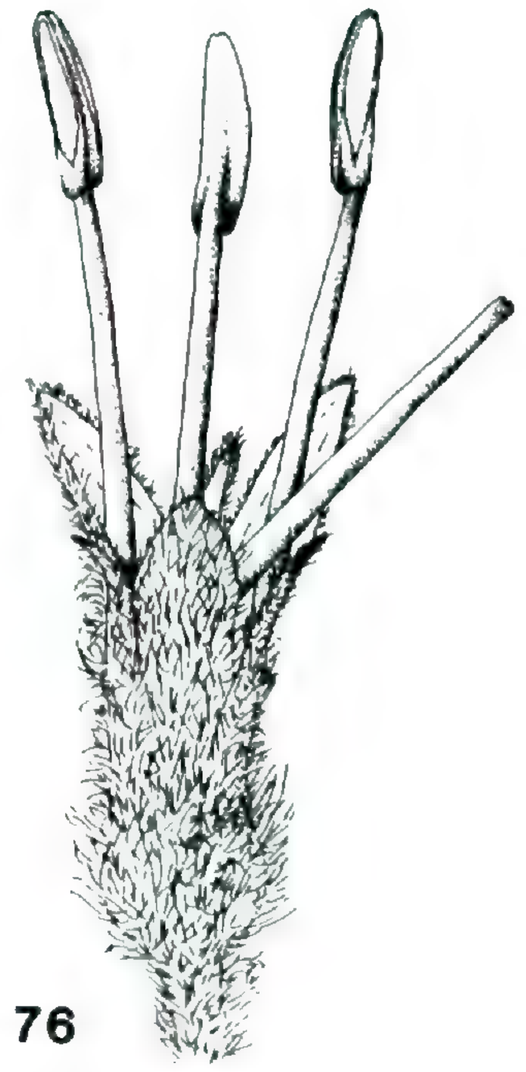
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FIGURES 71–76. Floral morphology in the Haemodoraceae.—71. *Barberetta aurea*; ×3.4. 72–73. *Dilatris corymbosa*.—72. Whole flower longitudinal section. Note inferior ovary; ×3.0.—73. Outer tepal. Note apical glands; ×3.4.—74. *Haemodorum spicatum*; ×3.4.—75. *Xiphidium coeruleum*; ×3.4.—76. *Lachnanthes caroliniana*; ×3.1.

fertile stamen, i.e., opposite the inner whorl of tepals, not the outer as in *Schiekia* (Fig. 50). The staminodia in *Pyrrorhiza* are thus hypothesized to be homologous with stamens of an inner whorl. Based on this interpretation, the assigned morphocline for stamen number in the Haemodoraceae is: 6 STAMENS ←[#21]→ 3 STAMENS + 2 LATERO-ANTERIOR STAMINODES ←[#22]→ 3 OR 1 STAMEN(S).

One difficulty with the above morphocline concerns *Schiekia* and *Pyrrorhiza*. Although *Schiekia* may be intermediate between a six-staminate and three-staminate condition (because of the presence of two latero-posterior staminodia), it is more likely intermediate between a three-staminate condition and the one-staminate morphology of *Pyrrorhiza*. This latter interpretation is based on the presence in *Schiekia* of two reduced latero-posterior stamens with caducous anthers that greatly resemble and are likely homologous with the two staminodia of *Pyrrorhiza*. However, so as not to bias the present study, the latter hypothesis is treated as an independent character (see *Stamen dimorphism*).

In general, fewer than six stamens in monocotyledons is a condition thought to have arisen by reduction from the ancestral condition of six stamens in two whorls (Dahlgren & Clifford, 1982); however, such generalized trends must be viewed with caution. With regard to outgroup comparison, all members of the Philydraceae have one stamen per flower, which interestingly is median anterior in position (similar to that in, e.g., *Pyrrorhiza*). The Pontederiaceae can have either six, three, or one stamen(s) per flower and are coded as polymorphic ("?").

Characters #23–25. Stamen dimorphism. In the members of the Haemodoraceae with six stamens, all six anthers are of equal size. However, of the taxa with three anther-bearing stamens, in *Dilatris* (Fig. 72), *Haemodorum* (Fig. 74), *Schiekia* (Figs. 47–50), and *Xiphidium* (Fig. 75), the anther of the adaxial stamen (relative to cyme axis) is significantly larger than those of the abaxial stamens. (*Schiekia* also has two staminodia; see characters #21, 22, *Stamen number*.) All three stamens and anthers are equal in the other genera with three stamens: *Barberetta* (Fig. 71), *Lachnanthes* (Fig. 76), and *Wachendorfia* (Figs. 51, 52). The filament of the odd stamen may be either longer (*Haemodorum*, *Schiekia*, and *Xiphidium*) or shorter (*Dilatris*) than the filaments of the two

equal stamens. Because of the positional similarity of the odd anther, however, these are all viewed as homologous features. In *Schiekia* the median anterior stamen is considerably enlarged relative to the two latero-posterior stamens (Fig. 47). The anthers of the two latero-posterior stamens of *Schiekia* are somewhat caducous (Figs. 47, 49), and the filaments of these stamens greatly resemble the staminodia of *Pyrrorhiza* (Figs. 44, 45). Therefore, it is hypothesized here that the two latero-posterior stamens of *Schiekia* are homologous (and evolutionarily intermediate) to the two latero-posterior staminodia of *Pyrrorhiza*. Furthermore, the occurrence of two latero-posterior staminodia in *Pyrrorhiza* may be interpreted as an extreme endpoint in anther dimorphism. Thus, a hypothesized morphocline for anther dimorphism in the family is: ANTHERS OF EQUAL SIZE ←[#23]→ 1 LARGE ANTERIOR + 2 SMALL POSTERIOR ANTHERS ←[#24]→ 1 LARGE ANTERIOR + 2 CADUCOUS LATERO-POSTERIOR ANTHERS ←[#25]→ 1 ANTERIOR ANTHER + 2 LATERO-POSTERIOR STAMINODIA.

Among the outgroup families stamen dimorphism (or apparent stamen reduction) is common. All species of the Philydraceae have a single stamen in posterior position, as is the odd stamen in the dimorphic members of the Haemodoraceae. However, because the homology of stamen dimorphism in the Philydraceae is uncertain, and because the presence of a single stamen in this family was taken into account previously (characters #21, 22, *Stamen number*), the Philydraceae were coded as uncertain ("?") for characters #23–25. Anther dimorphism varies considerably in the Pontederiaceae. Some species exhibit no anther dimorphism. Dimorphic stamens are present in *Heteranthera*, *Monochoria*, *Pontederia*, and *Scholleropsis*; in *Heteranthera* there is usually one large anterior stamen and two smaller latero-anterior stamens. (Note the positional difference to that in the Haemodoraceae.) In some *Heteranthera* species and in *Hydrothrix* of the Pontederiaceae, only one stamen is present. The Pontederiaceae are coded as polymorphic ("?") for characters #23–25.

Character #26. Stamen connective appendages. Distinctive lobed appendages are present on the upper abaxial stamen connective in all species of *Tribonanthes* (Fig. 59). Such stamen appendages are not found in the family or outgroups, although *Anigozanthos* may have mucronate anthers.

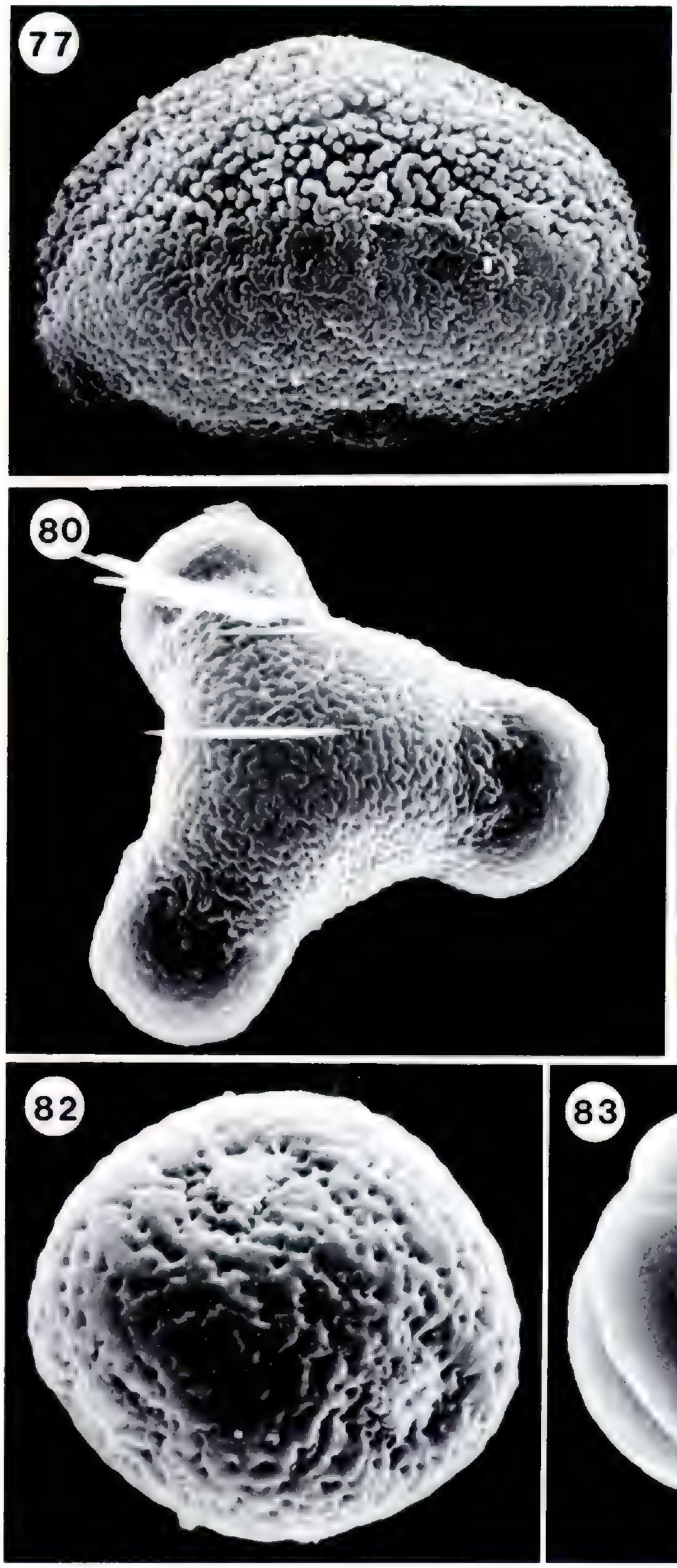
Characters #27, 28. Pollen aperture. Eight genera of the Haemodoraceae have a monosulcate pollen aperture type, as in *Haemodorum* (Fig. 77), whereas six genera have porate apertures (Figs. 78–80, 82; see Simpson, 1983). Of the latter, five genera have 2–3 apertures (Figs. 78–80). *Tribonanthes* differs in having 5–7 porate apertures (i.e., oligoforaminate; Fig. 82). Thus, this character is coded as: MONOSULCATE ←[#27]→ 2–3-PORATE ←[#28]→ OLIGOFORAMINATE.

Of the six genera with porate pollen apertures, four (*Anigozanthos*, *Blancoa*, *Conostylis*, and *Macropidia*) are similar in having protruding, hemispheric aperture walls essentially devoid of exine (Figs. 78, 80); the other two genera, *Phlebocarya* (Fig. 79) and *Tribonanthes* (Fig. 82), have rather flattened aperture walls with scattered exinous elements (Simpson, 1983). Although this additional feature is not taken into account in the character coding, it will be discussed after the cladistic analysis.

A monosulcate aperture type is considered to be ancestral for both the monocotyledons and the angiosperms (Zavada, 1983b; Walker & Doyle, 1975) and is likely ancestral for the Haemodoraceae. Among the outgroup taxa, all members of the Philydraceae have a monosulcate aperture (illustrated by *Helmholtzia* in Fig. 81; see Simpson, 1985a). All members of the Pontederiaceae have disulculate apertures (illustrated by *Pontederia* in Figs. 83, 84; see Simpson, 1987). Because the disulculate aperture type in the Pontederiaceae is probably derived from a monosulcate condition, and is almost certainly not homologous with the diporate aperture type in the Haemodoraceae, the Pontederiaceae are coded as having the equivalent of a monosulcate aperture type.

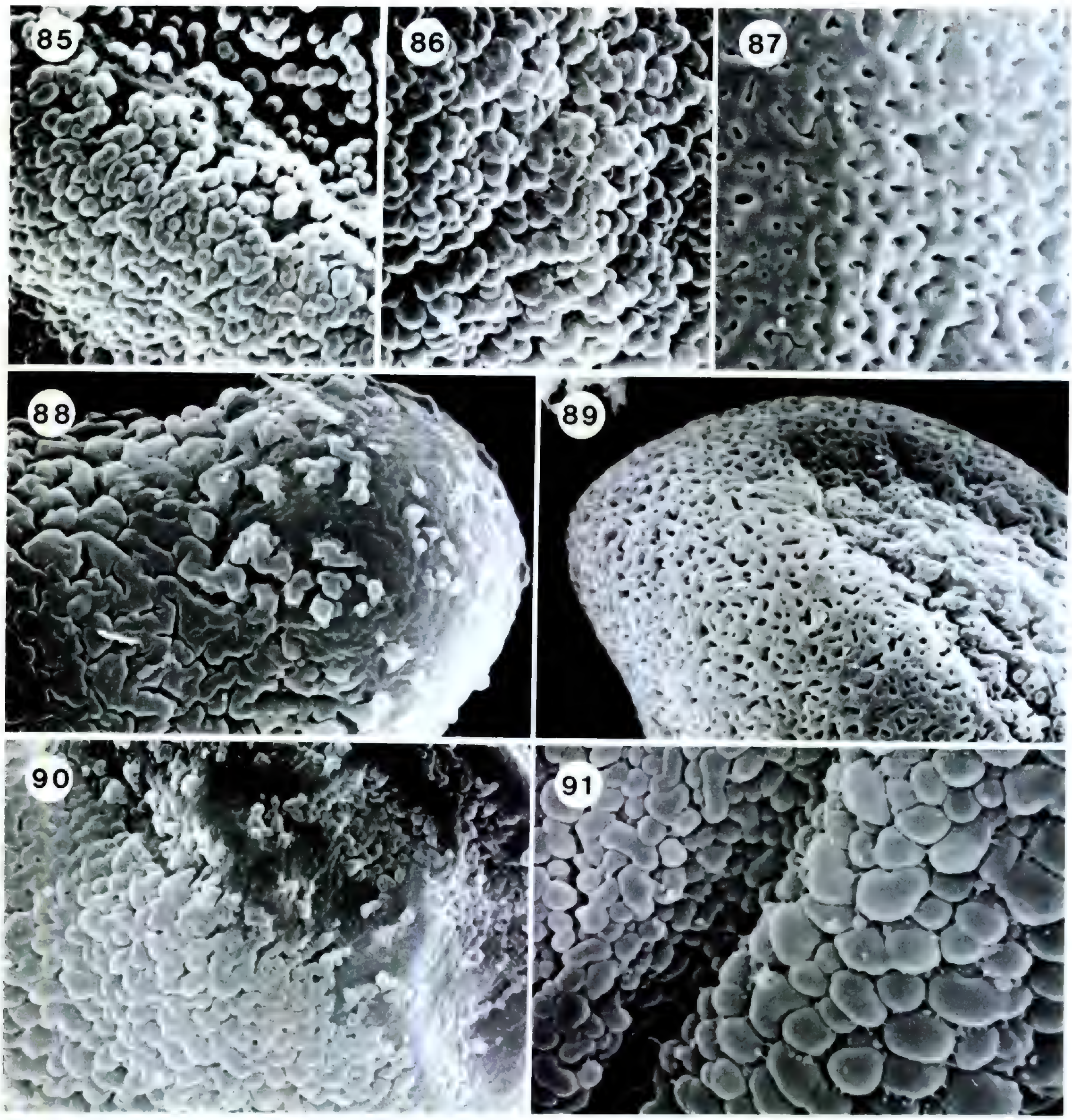
Characters #29, 30. Pollen sculpturing. Seven genera of the Haemodoraceae (all with monosulcate apertures) possess verrucate exine wall sculpturing, consisting of appressed wart-like projections of exine (illustrated by *Haemodorum* in Fig. 85 and by *Dilatris* in Fig. 86). *Schiekia*, also monosulcate, differs from the above in having foveolate sculpturing with minute outer pores (Fig. 87). Six genera of the family, all of which have porate apertures, have distinctive rugulate (brainlike) exine sculpturing (Fig. 88; see Simpson, 1983).

All three types of pollen wall sculpturing seen in the Haemodoraceae are found in the outgroups. Within the Philydraceae three of four genera have foveolate (to reticulate) sculpturing (Fig. 89), which somewhat resembles *Schiekia*; *Philydrella* of the Philydraceae possesses what is described as a rugulate sculpturing, but which does not greatly re-



FIGURES 77–84. Pollen shape and aperture morphology in the Haemodoraceae and outgroups.—77. *Haemodorum spicatum* (monosulcate); ×3,320.—78. *Anigozanthos flavidus* (diporate with hemispheric apertures); ×1,110.—79. *Phlebocarya ciliata* (diporate); ×2,160.—80. *Conostylis beliana* (triporate with hemispheric apertures); ×1,390.—81. *Helmholtzia acorifolia* (monosulcate); ×2,570.—82. *Tribonanthes variabilis* (oligoforaminate); ×1,760. 83–84. *Pontederia cordata* (disulculate);—83; ×1,630.—84. ×970.

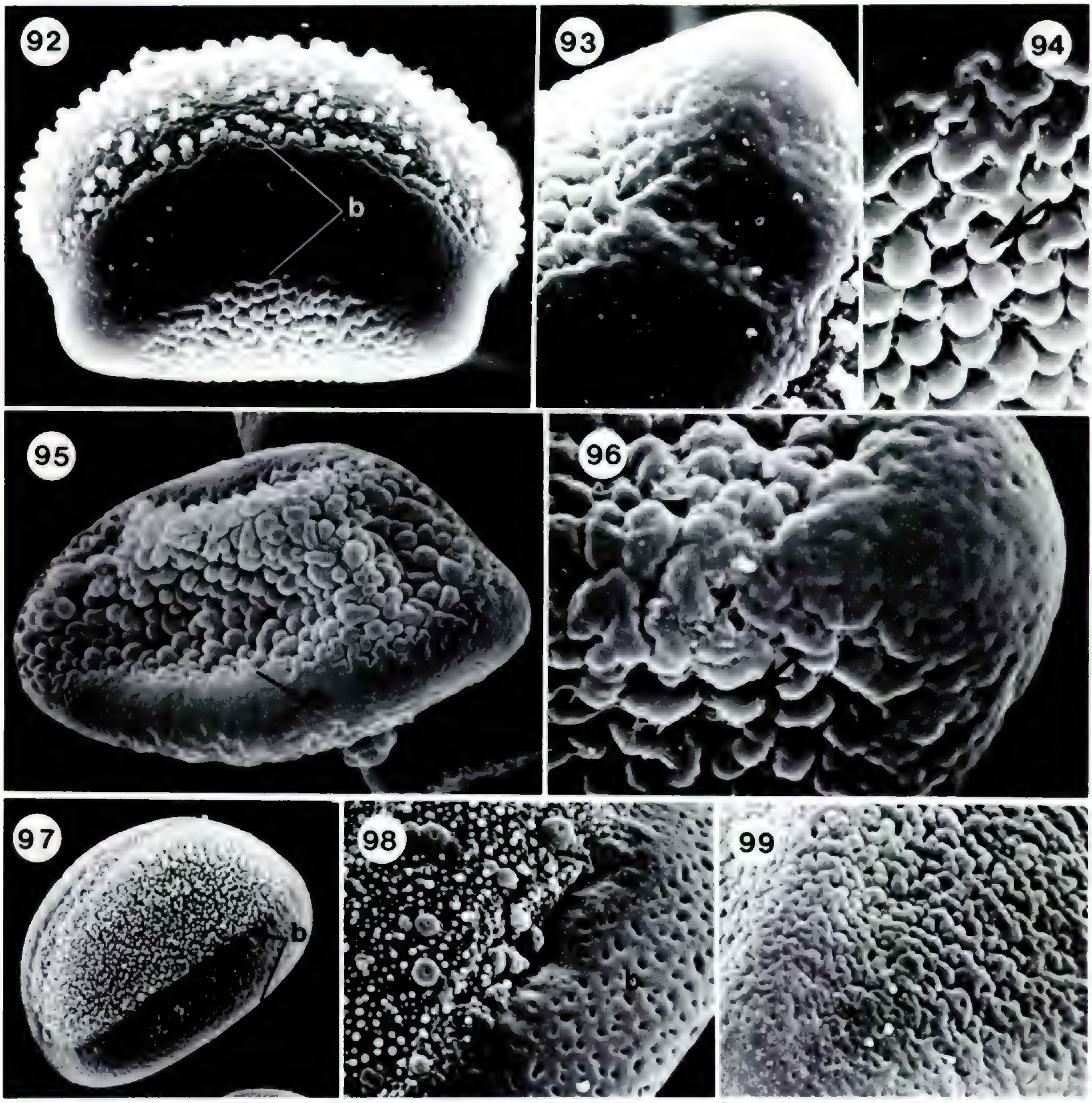
semble the rugulate sculpturing found in six genera of the Haemodoraceae (see Simpson, 1985a). Because the Philydraceae have two of the sculpturing types of the Haemodoraceae, they are coded as polymorphic ("?") for both characters. In fact, it seems quite likely that the resemblance in sculpturing between the Philydraceae and the Haemodoraceae is homoplasious anyway, as all Philydraceae have a quite different exine structure (see below, *Exine wall structure*). In the Pontederiaceae all investigated genera except *Pontederia* have verrucate sculpturing (illustrated for *Heteranthera*



FIGURES 85–91. Pollen wall sculpturing in the Haemodoraceae and outgroups.—85. *Haemodorum spicatum* (verrucate); ×6,610.—86. *Dilatris pilansii* (verrucate); ×4,400.—87. *Schiekia orinocensis* (foveolate); ×8,090.—88. *Anigozanthos flavidus* (rugulate); ×2,420.—89. *Helmholtzia acorifolia* (foveolate-reticulate); ×4,740.—90. *Heteranthera reniformis* (verrucate); ×2,480.—91. *Zosterella dubia* (verrucate); ×5,970.

in Fig. 90 and *Zosterella* in Fig. 91), which is virtually identical to that found in seven genera of the Haemodoraceae. In view of the similarity of exine structure between the Pontederiaceae and the verrucate Haemodoraceae (see *Exine wall structure*), it is very probable (and is coded as such) that the two families are homologous in terms of exine sculpturing as well.

The most likely morphocline for pollen sculpturing in the Haemodoraceae seems to be the following: FOVEOLATE ←[#29]→ VERRUCATE ←[#30]→ RUGULATE. Although the intergradation between the sculpturing types is not clear in itself, it is quite probable that the verrucate sculpturing type is ancestral for the Haemodoraceae as a whole, evidence for this being the identical sculpturing type (and exine structure; see below) in the Pontederiaceae. Thus, the rugulate and foveolate sculpturing types in the Haemodoraceae are hypothesized to have evolved independently from an ancestral verrucate type (to be tested by the cladistic analysis).



FIGURES 92–99. Palynological features in the Haemodoraceae. 92–94. *Wachendorfia thyrsiflora*.—92. Whole pollen grain, aperture above. Note psilate, micropore-pitted aperture border (b) and enlarged proximal verrucae (below); ×1,460.—93. Close-up of aperture border (b) and proximal verrucae (upper left); ×2,710.—94. Close-up of enlarged proximal verrucae (arrow); ×5,070. 95–96. *Barberetta aurea*.—95. Whole pollen grain, aperture facing. Note psilate, micropore-pitted aperture border (b); ×2,430.—96. Proximal surface, showing aperture border (b) and enlarged proximal verrucae (arrow); ×5,090. 97–99. *Dilatris corymbosa*.—97. Whole pollen grain, aperture facing, showing aperture border (b); ×925.—98. Close-up of psilate, foveolate aperture border (b); ×2,460.—99. Close-up of proximal surface. Note absence of enlarged verrucae; ×2,570.

Character #31. Pollen apertural border. Smooth pollen grain apertural borders, consisting of a band of psilate material with minute perforations, are present in *Wachendorfia* (Figs. 92, 93), *Barberetta* (Figs. 95, 96), and *Dilatris* (Figs. 97, 98). The pollen apertural borders in *Dilatris* differ slightly from those in the other two genera in having larger perforations (being "foveolate") in contrast to the micropores present in *Barberetta* and *Wachendorfia*. Because of their overall similarity, all three genera are coded as possessing this feature. Similar pollen grain apertural borders are absent in other investigated members of the Haemodoraceae, although a tendency for such a border may be seen in *Xiphidium* (Simpson, 1983). An apertural border is absent also in all investigated members of the Philydraceae (Simpson, 1985a) and Pontederiaceae (Simpson, 1987).

Character #32. Pollen with large proximal verrucae. Large verrucate exine elements are present on the proximal pollen grain surface of *Barberetta* (Fig. 96) and *Wachendorfia* (Figs. 92–94). Similar elements do not occur elsewhere in the family or among any investigated outgroups. In particular, *Dilatris*, which resembles *Barberetta* and *Wachendorfia* in having a pollen apertural border, lacks any indication of enlarged verrucate elements on the proximal pollen grain surface (see Fig. 99).

Characters #33–37. Exine wall structure. Five basic types of pollen grain exine wall structure can be identified in the Haemodoraceae (see Simpson, 1983). *Lachnanthes* (Figs. 100, 101) and *Haemodorum* (Fig. 102) have a "one-layered" exine structure, consisting of baculate (rod-shaped) elements that are closely appressed and generally basally fused. Ten other genera of the family have a two-layered exine wall, with inner and outer layers delimited by a distinctive "commissural line" (Figs. 103, 104); these inner and outer exine layers are ektexinous based on cytochemical tests and have similar TEM staining properties (Simpson, 1983). Of these ten genera, six differ in having an inner exine layer composed of papillate exinous elements (Fig. 104), while those of *Phlebocarya* are restricted to the apertural region. *Pyrrorhiza* (Fig. 105) and *Schiekia* (Fig. 106) possess, respectively, two- and three-layered exine walls. These two genera resemble one another (and differ from other family members) in that the subexterior exine wall is granular and discontinuous in composition.

In *Haemodorum* and *Lachnanthes*, the single-layered exine wall resembles and is probably homologous with the outer exine layer of those taxa that have a two-layered structure. In fact, the pollen exine wall of *Haemodorum* has an occasional scanty inner exine layer, perhaps indicative of an ancestral inner layer (Simpson, 1983). (Developmental studies to test this hypothesis are in progress by the author.) Similarly, in *Pyrrorhiza* and *Schiekia* the outermost layer of exine is probably structurally homologous to the single exine layer of *Haemodorum* and *Lachnanthes*. This can be seen near the apertural region, where all but the outermost exine layer disappears (Simpson, 1983).

As seen in Figure 112 (after Simpson, 1983), a gradation among observed exine wall structural types of genera in the Haemodoraceae can be identified. However, because of the uncertainty of some of the intergrading states of this morphocline, and because its length could possibly bias the study, the character "exine wall structure" was divided into the following two-state (absence or presence) characters:

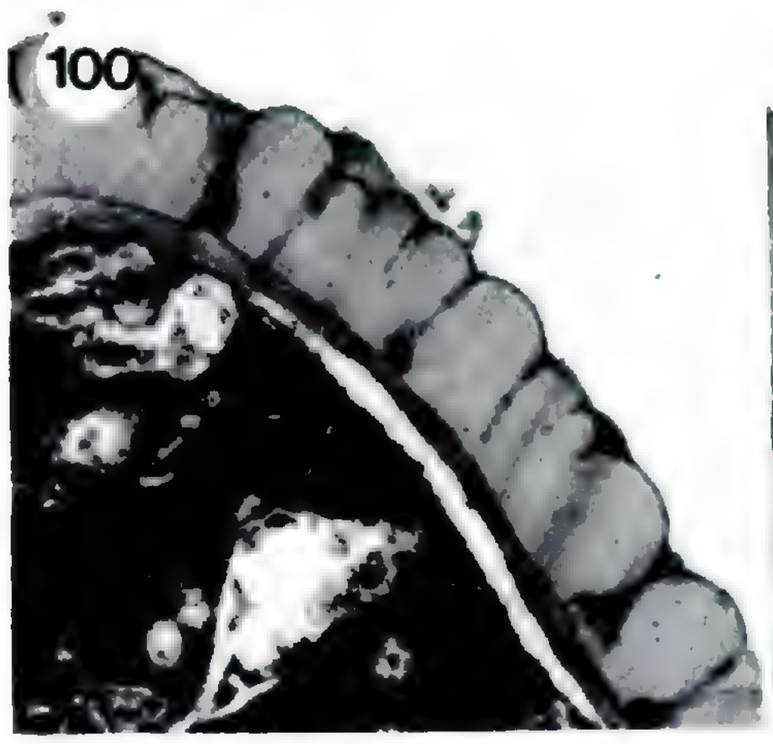
Characters #33, 34: Number of exine wall layers, coded as the following linear morphocline: 1-LAYERED ←[#33]→ 2-LAYERED ←[#34]→ 3-LAYERED.

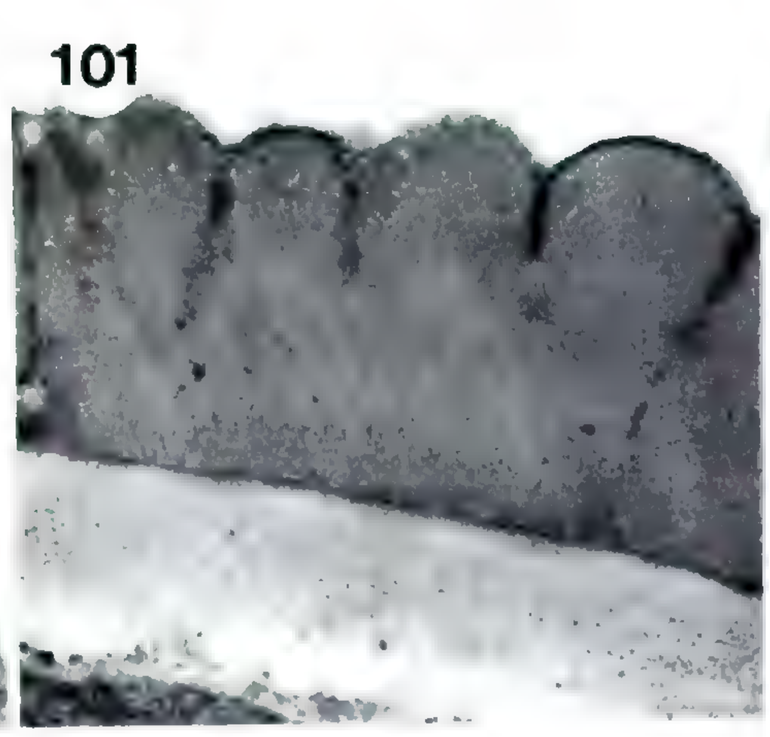
Character #35: Exine wall, if two-layered, with papillate inner exine elements. This includes *Phlebocarya*, which possesses papillate inner exine elements only near the apertural region. Taxa without a two-layered exine (*Haemodorum*, *Lachnanthes*, and *Schiekia*) are coded as "X."

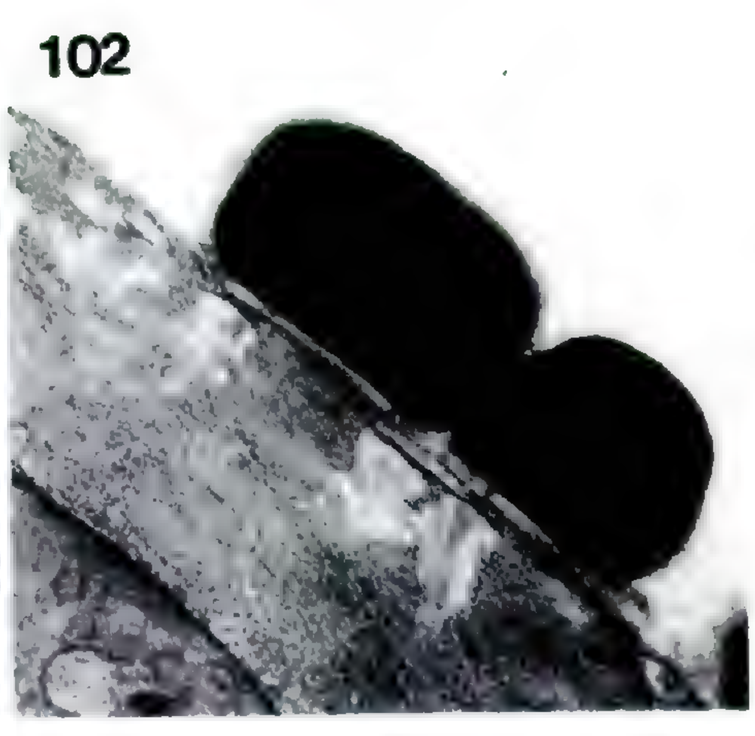
Character #36: Exine wall, if two-layered, with only papillate elements making up the inner wall. This condition is present in *Anigozanthos*, *Blancoa*, *Conostylis*, *Macropidia*, and *Tribonanthes*. Again, the three taxa which lack a two-layered exine are coded as "X."

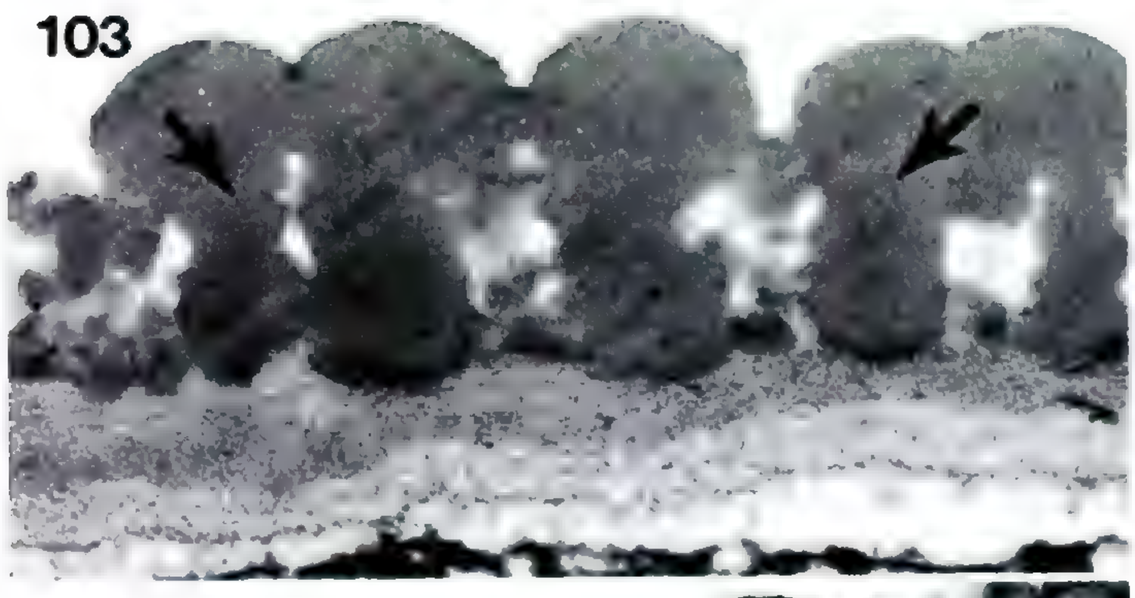
Character #37: Subexterior exine wall discontinuous. This feature links the common exine morphology of *Pyrrorhiza* and *Schiekia*. Figure 165B illustrates the character coding for exine wall structure (characters #33–37).

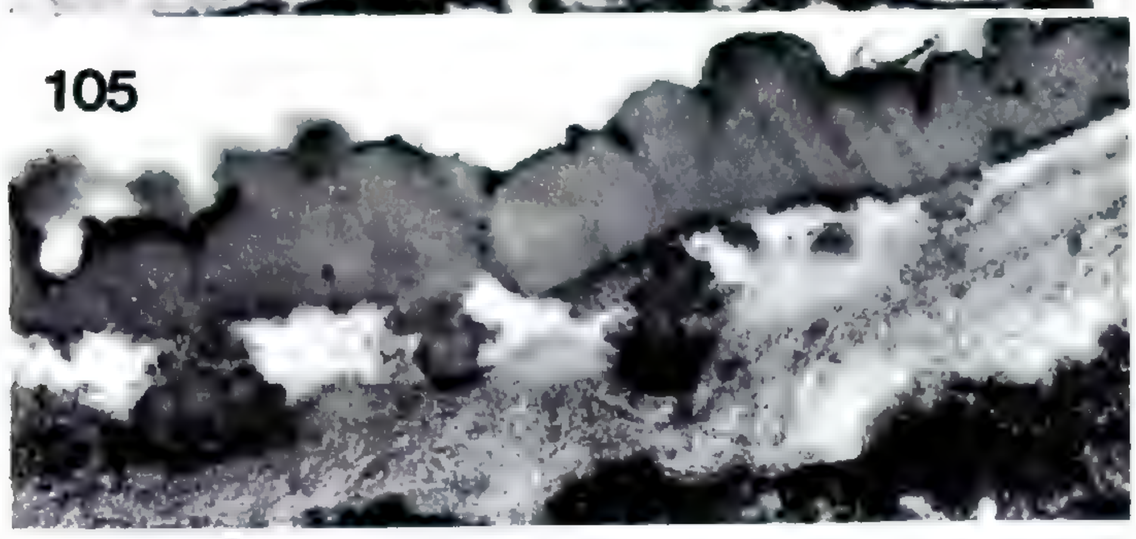
Among the outgroups, all Philydraceae have a typical homogeneous tectate-columellate exine structure (Fig. 107) with characteristic lamellar deposits inner to the foot-layer (see Simpson, 1985a). The directionality of the tectate-columellate exine structure with reference to the specific types occurring in the Haemodoraceae is uncertain; thus, the Philydraceae are coded as having uncertain homology ("?") for characters #33–37. In contrast, several members of the Pontederiaceae have an exine structure very similar to that in the Haemodoraceae (see Simpson, 1987). A "one-layered" exine structure, identical to that of *Haemodorum* and *Lachnanthes* of the Haemodoraceae, is seen in two genera of the Pontederiaceae: *Eichhornia* and *Hydrothrix* (Fig. 110). *Heteranthera*, *Reussia*, and *Zosterella* (Fig. 111) of the Pontederiaceae have a two-layered exine with a "commissural line" delimiting inner and outer layers, resembling that found in ten genera of the Haemodoraceae. Four genera of the Pontederiaceae, *Heteranthera*, *Monochoria* (Fig. 108), *Pontederia* (Fig. 109), and *Scholleropsis*, have what is described as a tectate-columellate exine structure. However, in these taxa the foot-layer is thin or discontinuous, the columellae are short and ill-defined, and the tectum is thick and composed of rod-shaped elements (resembling the rod-shaped elements of the verrucate members of the Hae-

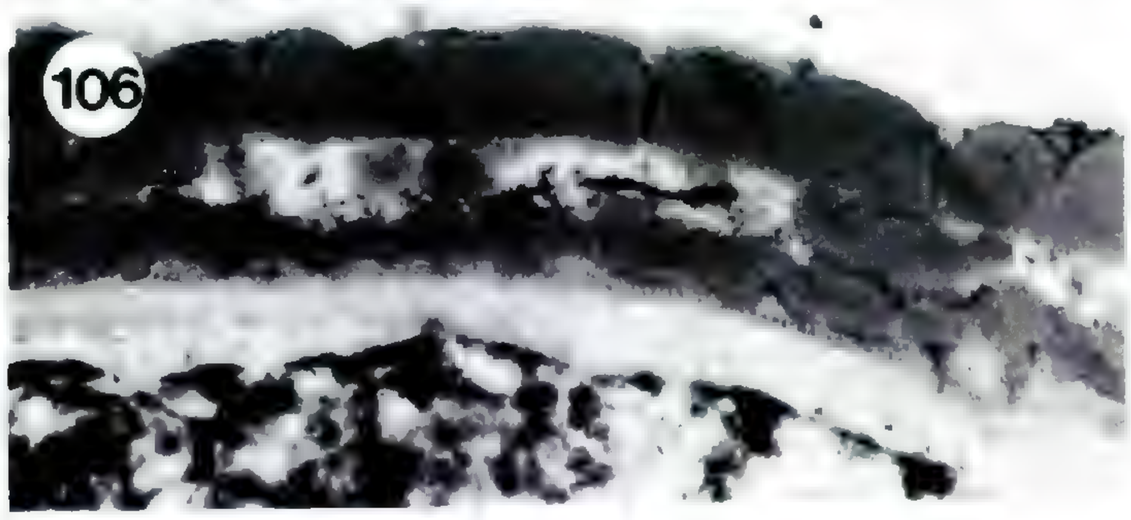












FIGURES 100–111. Exine wall ultrastructure in the Haemodoraceae and outgroups.—100, 101. *Lachnanthes caroliniana* (one-layered exine composed of laterally appressed and basally fused rod-shaped elements); ×11,400 (100), ×26,200 (101).—102. *Haemodorum simplex* (one-layered, composed of laterally appressed rod-shaped elements); ×29,900.—103. *Xiphidium coeruleum* (two-layered exine, inner layer papillate; note commissural line at arrows); ×20,700.—104. *Tribonanthes variabilis.* (two-layered exine, inner layer papillate; note commissural

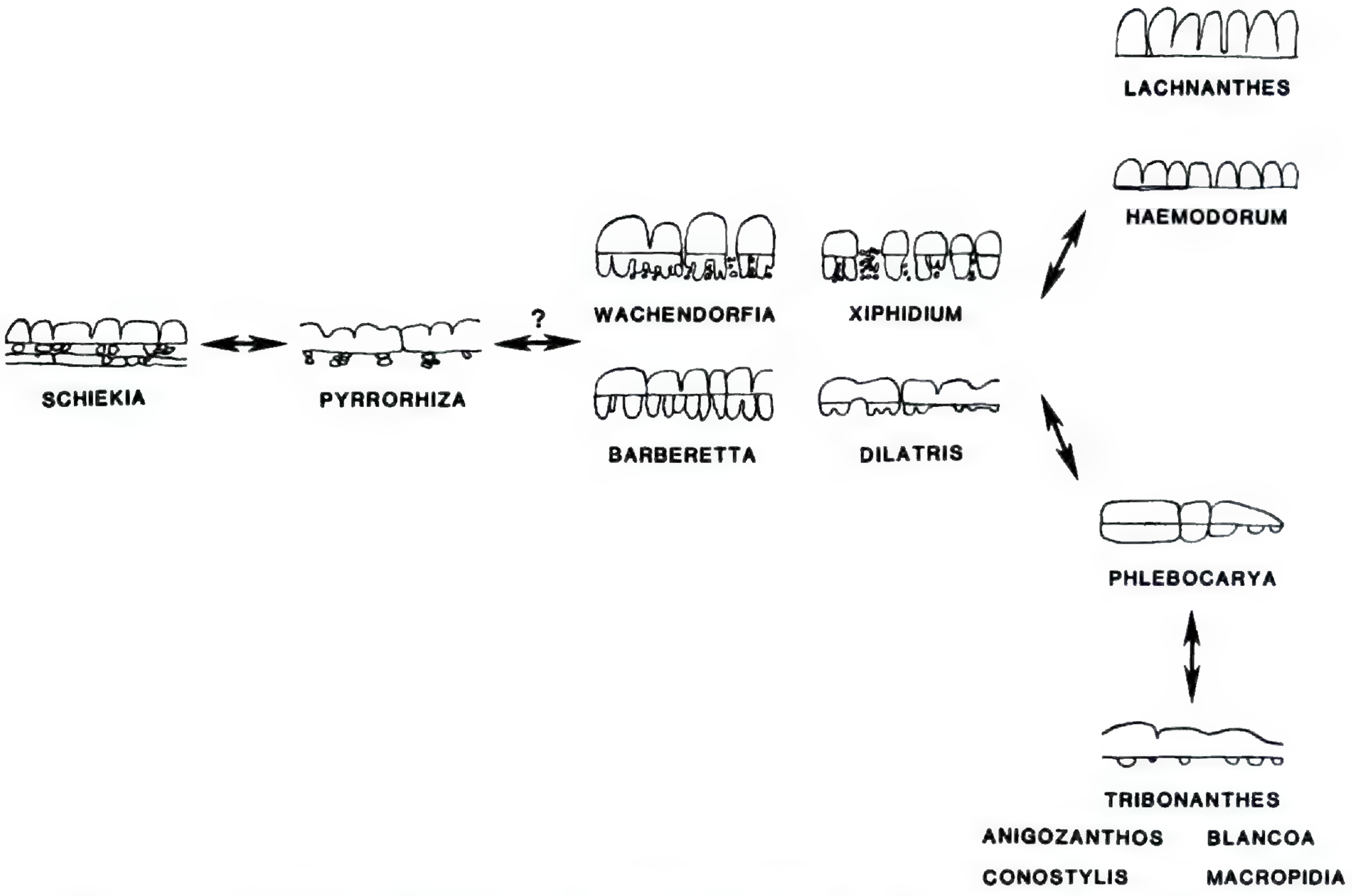


FIGURE 112. Hypothesized intergradation series of exine ultrastructure morphology in the Haemodoraceae. Note uncertainty as to homology of two-layered exine of *Pyrrorhiza*.

modoraceae). Thus, Simpson (1987) proposed that this "modified" tectate-columellate exine structure in the Pontederiaceae may not be homologous with the more typical tectate-columellate structure (e.g., in the Philydraceae and in many other monocots) and may have been secondarily derived from an exine structure comprised of rod-shaped elements. (Developmental studies are underway by the author to test this hypothesis.) Because both a one-layered exine and a two-layered exine (with a delimiting "commissural line") occur in the Pontederiaceae, this outgroup is coded as polymorphic ("?") for characters #33 and #35, 36. Character #34 is coded as lacking (state 0) a three-layered exine, and character #37 is coded as lacking (state 0) a discontinuous subexterior exine wall.

Character #38. Enantiostyly. Enantiostyly is the curvature of the style to either the right or left, thus defining so-called "right-handed" and "left-handed" flowers. Displacement of one or more stamens usually accompanies enantiostyly, which results in an asymmetric flower. In the Haemodoraceae several genera exhibit enantiostyly. All five species of the zygomorphic *Wachendorfia* have enantiostylous flowers, in which the arcuate style is deflected to one side of the flower and the median anterior stamen is deflected to the other side (Fig. 51). Ornduff & Dulberger (1978) have hypothesized that such stylar enantiomorphy functions to promote pollination between flowers of different morphs, in effect promoting outcrossing. Flowers of *Schiekia* have a similar enantiostyly in which the style and median anterior stamen are oppositely displaced (Fig. 47); the two latero-posterior stamens (unlike those of *Wachendorfia*) are considerably smaller. Both *Schiekia* and *Wachendorfia* have what are presumed to be nectar guides near

←

line at arrows); ×17,700.—105. *Pyrrorhiza neblinae* (two-layered exine; note amorphous, discontinuous inner exine layer); ×19,400.—106. *Schiekia orinocensis* (three-layered exine; note amorphous and discontinuous middle layer); ×21,200.—107. *Orthothylax glaberrimus* (tectate-columellate exine with lamellae inner to foot-layer); ×38,600.—108. *Monochoria vaginalis* (tectate-columellate exine with ill-defined interstitial layer); ×24,300.—109. *Pontederia cordata* (tectate-columellate exine with discontinuous foot-layer); ×18,500.—110. *Hydrothrix gardneri* (one-layered exine composed of laterally appressed and basally fused rod-shaped elements); ×39,000.—111. *Zosterella dubia* (two-layered exine, inner layer papillate; note commissural line at arrows); ×13,900.

the base of the posterior tepals. Thus, it is probable that in both of these genera (which have zygomorphic, horizontal flowers) an insect visitor would alight in a consistent orientation, forwardly directed toward the ovary base where nectar would collect. Pollen initially transferred to one side of the insect's body would, in subsequent visitations, more likely contact the stigma of a flower of opposite handedness (see Ornduff & Dulberger, 1978, re. *Wachendorfia*). *Pyrrorhiza*, the only other genus of the family with zygomorphic flowers (not caused by longitudinal splitting of the perianth; see *Perianth splitting*), does not possess enantiostyly. The style of *Pyrrorhiza* is relatively straight and is positioned directly above the single anterior stamen (Fig. 44).

Styles of four other family genera, *Barberetta* (Fig. 71), *Dilatris* (Fig. 72), *Lachnanthes* (Fig. 76), and *Xiphidium* (Fig. 75), also are strongly curved to one side of the flower. In *Haemodorum* the styles of adjacent flowers in a flower pair are each slightly incurved, forming mirror image pairs. These styles are only slightly curved and are not strongly displaced to one side (Fig. 74); however, they are probably homologous with the strongly displaced stylar curvature in the other six genera and are so coded. In contrast to *Schiekia* and *Wachendorfia*, however, the above genera have *actinomorphic* and *erect* (not zygomorphic and horizontal) flowers without any type of bilaterally symmetric nectar guides. It is, therefore, likely that an insect visitor to flowers of any of these four genera would be positioned inconsistently with regard to the deflected style. Enantiostyly in these taxa may be adaptive in simply decreasing the chance of self-pollination by physically displacing the stigma from anthers.

Among the outgroup taxa, enantiostyly occurs in all species of the Philydraceae. In fact, the style is displaced to one side of the (sole) anterior stamen, similar to enantiostyly in the Haemodoraceae. In the Pontederiaceae only *Heteranthera* and *Monochoria* have "weakly enantiostylous flowers" (Eckenwalder & Barrett, 1986); all other Pontederiaceae lack enantiostyly. The Pontederiaceae are thus coded as polymorphic ("?") for this character.

Character #39. Ovary position. Nine genera of the Haemodoraceae have an inferior ovary. Certain species of *Conostylis* have a *mostly* inferior ovary; these are coded as having inferior ovaries. The other five family genera clearly have superior ovaries.

Within the angiosperms as a whole, an inferior ovary is generally considered to be a derived feature (Bessey, 1915; Sporne, 1975), evolving possibly because of selective pressure by floral herbivores or pollinators (Grant, 1950) or in response to an adaptive advantage caused by increased protection of seeds or increased energy allocation to developing ovules (Stebbins, 1974). (See, however, Eyde & Tseng, 1969, regarding a possible case of derivation of a superior ovary from an ancestral inferior ovary.) All members of the two designated outgroups in this study have superior ovaries and are so coded.

Character #40. Septal nectaries. Within the Haemodoraceae all genera possess septal nectaries, with the exception of *Xiphidium*. In genera with inferior ovaries, the septal nectaries consist of slit-like channels, lined with a single epithelial layer, which traverse the septa at the upper part of the ovary and release nectar at the ovary apex near the base of the style. Among family members with inferior ovaries, *Dilatris* and *Phlebocarya* are exceptional in having extremely minute septal nectaries, consisting of a very short chamber located at the extreme ovary apex. Of the genera with superior ovaries, *Barberetta*, *Pyrrorhiza*, *Schiekia*, and *Wachendorfia* have very small septal nectaries, arising and opening up at the ovary base. In the case of *Schiekia* and *Wachendorfia*, nectar secretions presumably arise from these septal nectaries and collect in the two lateral "apertures" characteristic of these two genera. The complete absence of septal nectaries in *Xiphidium* (which has a superior ovary) may be correlated with the fact that it is visited by pollen-feeding, not nectar-feeding, bees via an anther vibrational ("buzz") mechanism (Buchmann, 1980). Thus *Xiphidium* may represent a specialization in which the selective pressure for nectar secretion was eliminated, establishing pollen as the primary visitor attractant. In view of the reduced septal nectaries in most superior-ovary taxa, it is not unreasonable to envision a loss of these structures in *Xiphidium*, particularly in light of its pollination mechanism.

Among the outgroup taxa, septal nectaries are absent from all four genera of the Philydraceae. Septal nectaries are present in at least *Eichhornia* and *Pontederia* of the Pontederiaceae but are absent in *Heteranthera* of that family (present study). The septal nectaries of the Haemodoraceae are very likely homologous with those in the Pontederiaceae and probably with those of numerous other monocots. However, because of their variability, the Pontederiaceae are coded as polymorphic ("?") for this character.

Character #41. Fertile carpels. All species of the Haemodoraceae have three connate carpels.

In the monotypic genus *Barberetta*, however, the seeds of two carpels abort during development; only the posterior carpel is fertile at maturity. Regularly aborting carpels are not found in any other members of the Haemodoraceae. (*Barberetta* is also unique in the family in having the style displaced laterally relative to the ovary apex; this displacement is certainly correlated with the development of only one carpel containing one ovule.)

Among the outgroup taxa, abortive carpels are absent in the Philydraceae. Abortive carpels are found only in *Pontederia* and *Reussia* of the Pontederiaceae, being absent in all other genera of the family. Thus, the Pontederiaceae are coded as polymorphic ("?") for this character.

Character #42. Locule number. All members of the Haemodoraceae have three locules, with the sole exception of *Phlebocarya*. Ovaries of *Phlebocarya* possess three basal, epitropous ovules with rudimentary or only partially protruding lateral septa and no apical septa. Thus, the ovary of *Phlebocarya* is technically uniloculate.

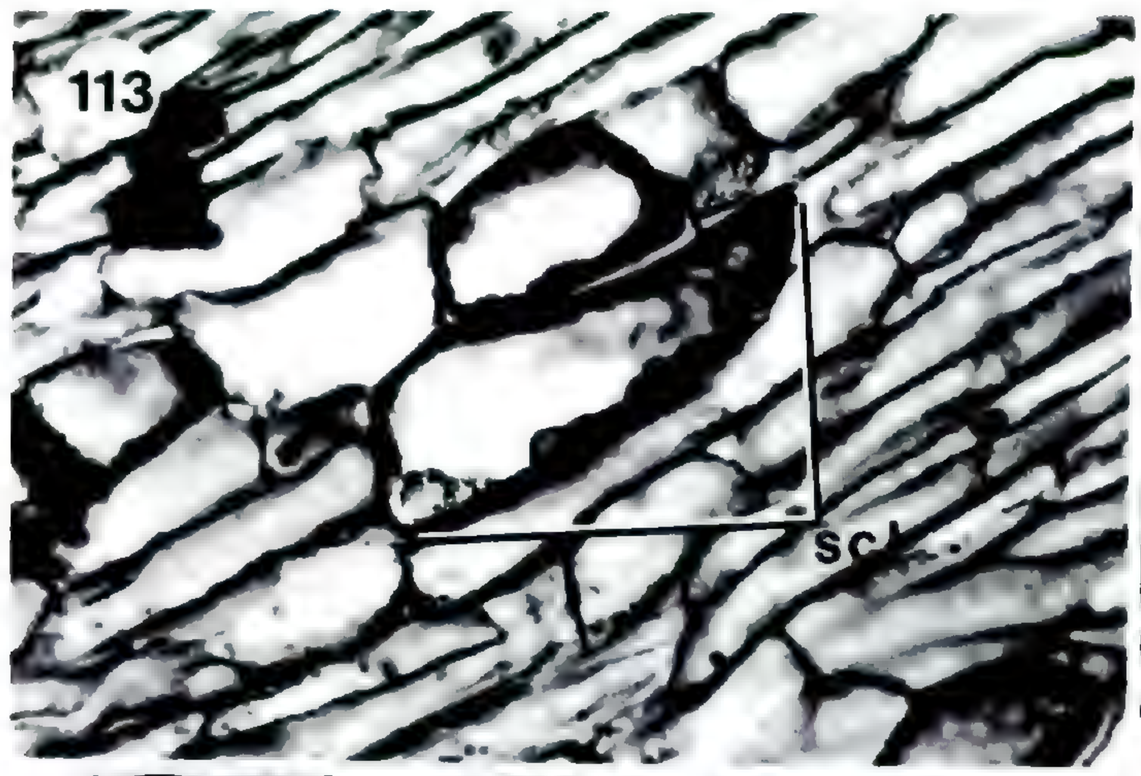
A three-loculate ovary is found in all members of the Pontederiaceae, and in all Philydraceae with the exception of *Philydrum*. Here most of the apical volume of the ovary is unilocular, with protruding, bibrachiate parietal placentae bearing numerous ovules. Thus the Philydraceae are coded as polymorphic ("?") for this character.

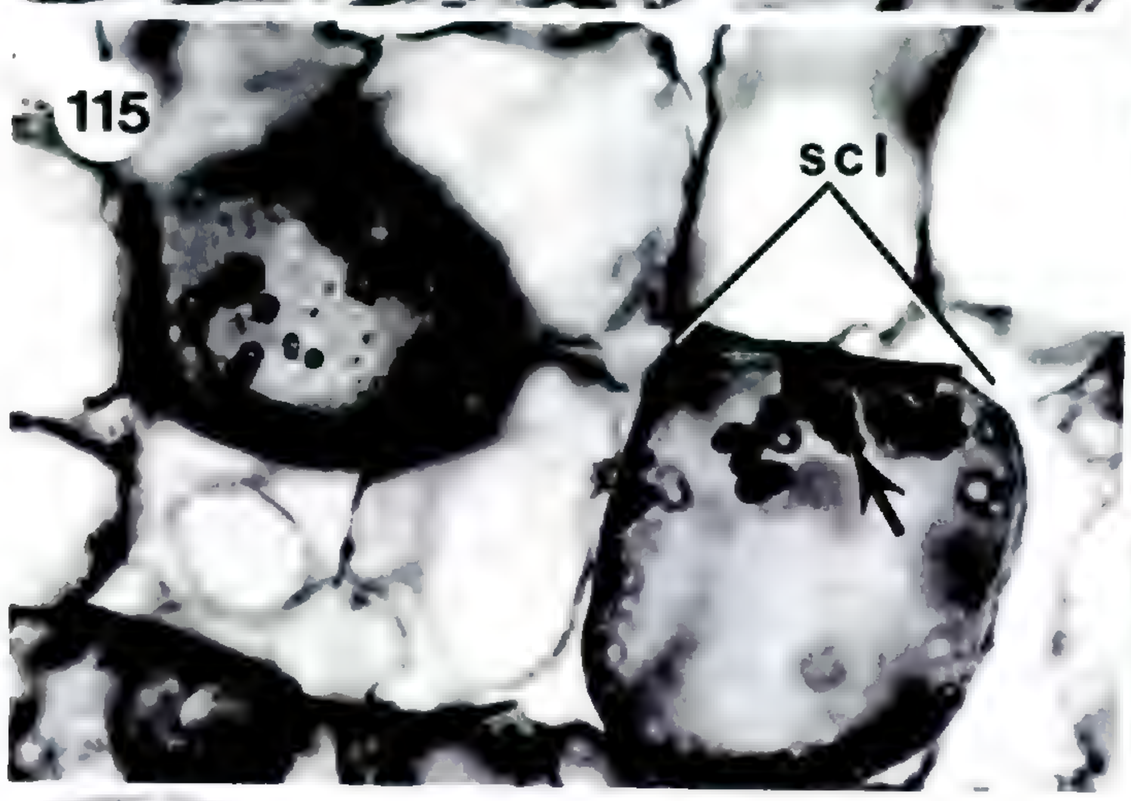
Character #43. Placental sclereids. Distinctive sclereids occur in the ovary placental tissues in six family genera: *Anigozanthos* (Figs. 113, 114), *Blancoa*, *Conostylis*, *Macropidia*, *Tribonanthes* (Fig. 115), and *Phlebocarya* (Fig. 116). These placental sclereids consist of isodiametric to slightly elongate (generally 3–4 times longer than broad) cells with moderately thick secondary cell walls. Characteristic of these sclereids are the presence of numerous spherical, nodulelike structures attached to the inner surface of the secondary cell wall (Figs. 114–116, 119, 120); both walls and nodules stain densely with safranin and are apparently lignified. The placental sclereids are distributed somewhat randomly, either singly or in small clusters, throughout the nonvascular tissue of placentae and styles and occasionally the ovary wall. Placental sclereids were not observed in any organ of the other eight family genera: *Barberetta*, *Dilatris*, *Haemodorum*, *Lachnanthes*, *Pyrrorhiza*, *Schiekia*, *Wachendorfia*, and *Xiphidium*.

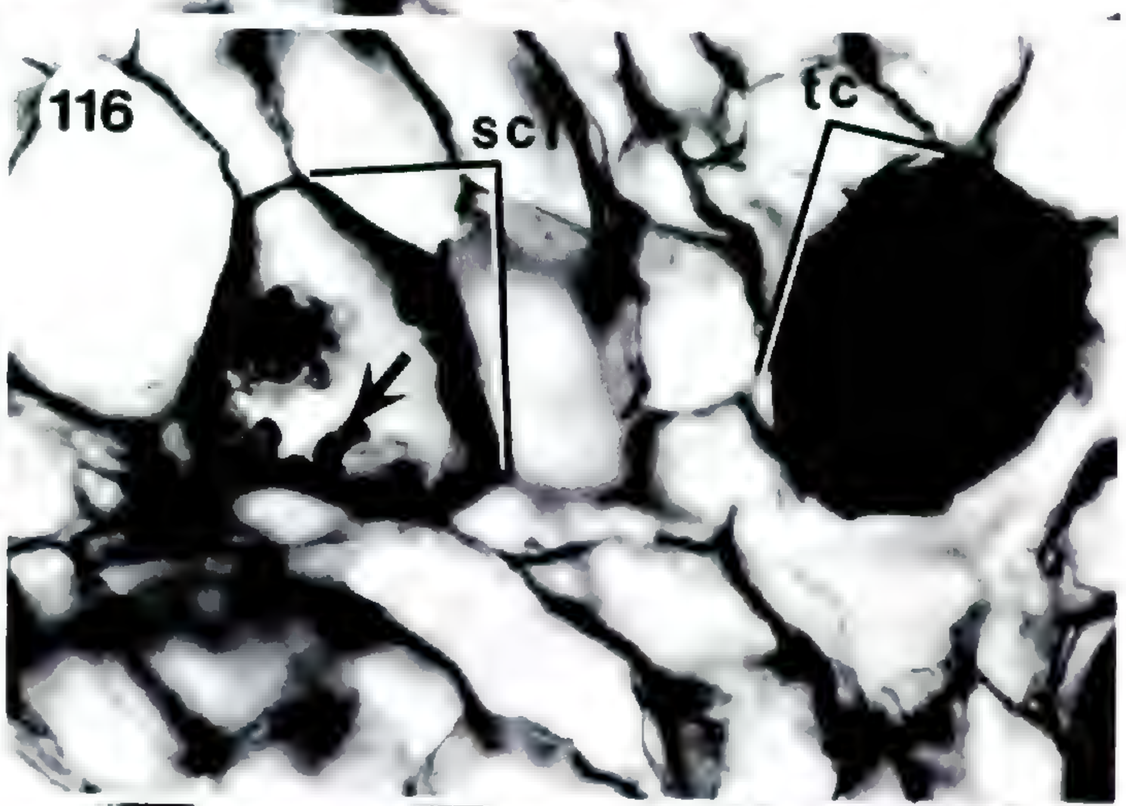
These characteristic placental sclereids are present in all four genera of the Philydraceae (illustrated by *Philydrum* in Figs. 117–119). These sclereids also occur in at least *Pontederia* of the Pontederiaceae (Fig. 120) but are absent in *Heteranthera reniformis* of that family. Despite the observed polymorphism, it seems very likely that the sclereids of the Pontederiaceae are homologous to those of the Haemodoraceae in view of their anatomical and positional similarity. Because the independent evolution of sclereids in the Pontederiaceae seems quite unlikely, this family is coded as having placental sclereids present.

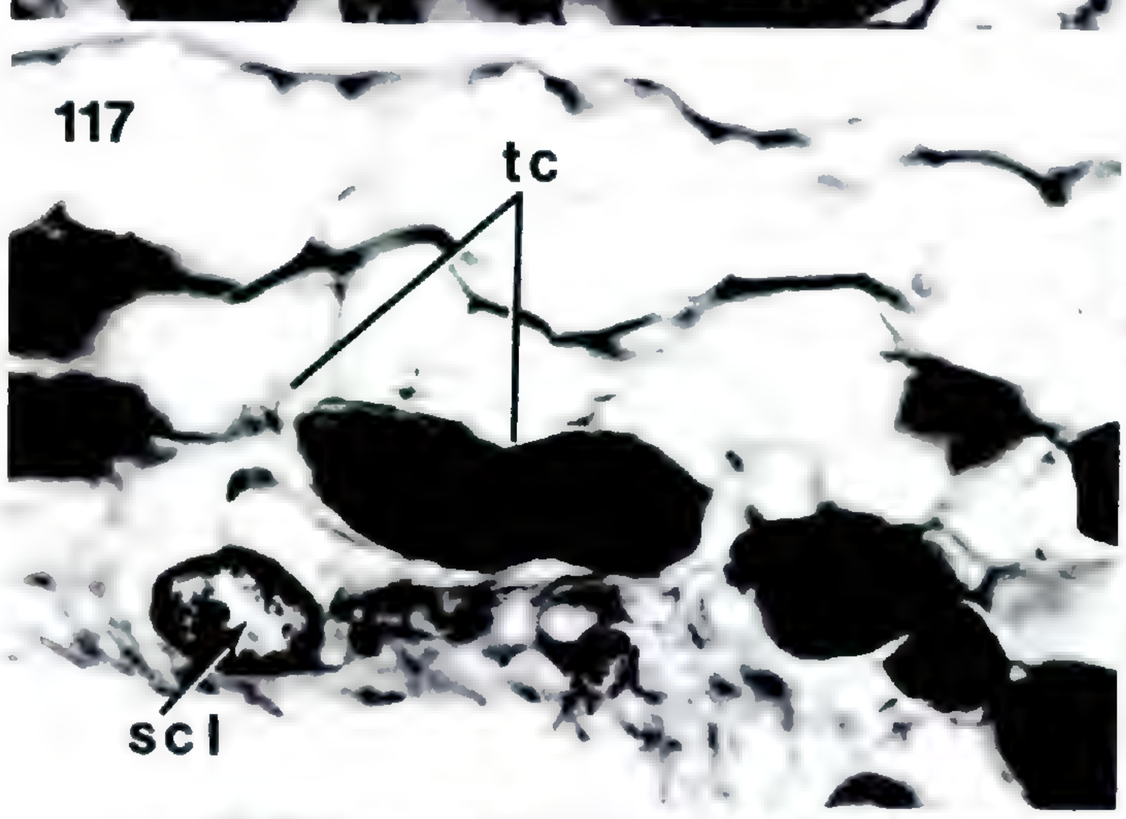
Of the above genera having placental sclereids, four also possess tannin cells in the ground tissue of ovary placentae: *Helmholtzia*, *Philydrum* (Fig. 117), *Phlebocarya* (Fig. 116), and *Pontederia* (Fig. 120); the remaining five genera possess *only* placental sclereids. These placental tannin cells are usually found in small clusters in the ground tissue of ovary placentae. They consist of generally isodiametric (occasionally slightly elongate) cells with thin, unlignified cell walls. The entire cell lumen of these cells is filled with an ergastic substance that stains very densely with safranin; this is characteristic of tanniniferous compounds (Johansen, 1940), though no specific chemical tests were made. These placental tannin cells are very similar to and very likely homologous with the perianth tannin cells discussed above (see *Perianth tannin cells*).

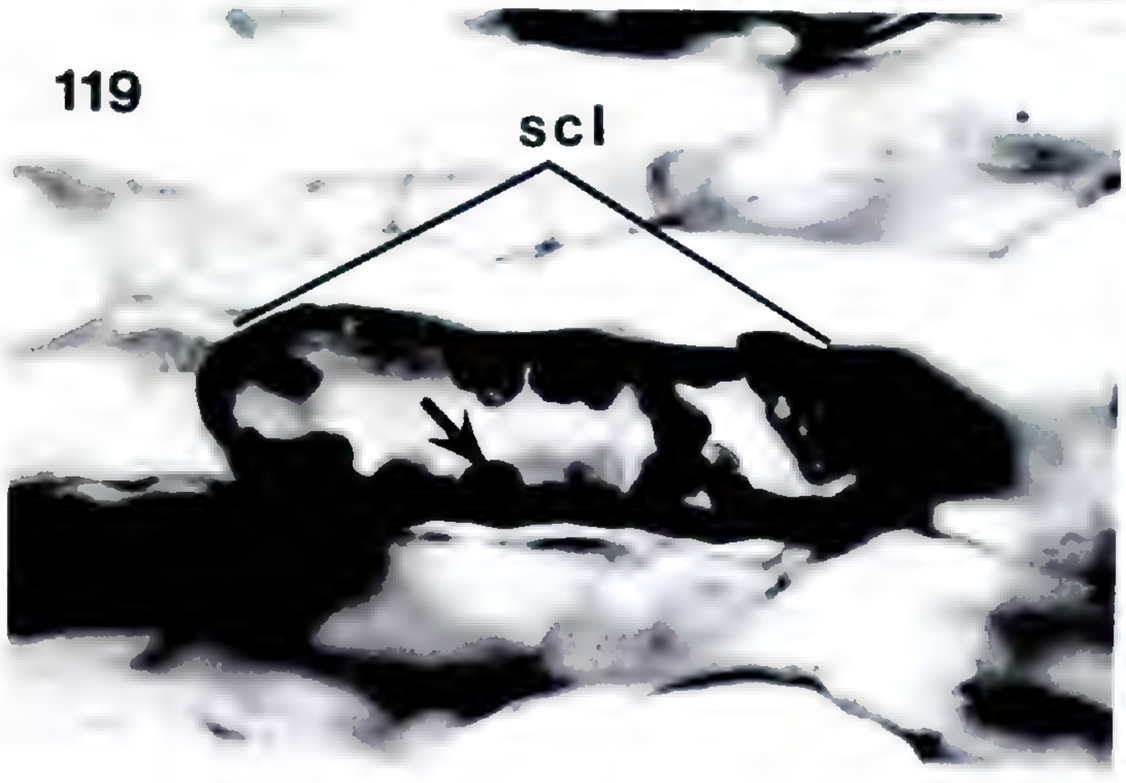
Characters #44–47. Ovule morphology and number. The morphology and number (per carpel) of ovules in the Haemodoraceae are quite variable (see Figs. 121–139). Virtually all ovules in the family have a narrow micropylar "neck" arising from the ovule body. The shape of the ovule body itself, however, can be somewhat globose, as in *Dilatris* (Fig. 122), *Haemodorum* (Fig. 124), and *Lachnanthes* (Fig. 123), or variably elongate and often flask-shaped. Placenta morphology, ovule position, and ovule number also vary. In most taxa the ovules are hypotropous in position, with the micropyle directed downward (proximally). *Phlebocarya* is the only genus of the family with epitropous ovules; these are arranged, one per carpel, in a ring, arising from the base of the ovary (Fig. 137). *Lachnanthes* (Fig. 123) and *Schiekia* (Fig. 126) are similar in having 5–7 and (3)4 ovules, respectively. These ovules are pleurotropously positioned (i.e., with the micropyle directed sidewise, towards the central flower axis) on a placenta that protrudes into the locule. This placenta is quite enlarged and peltiform in *Lachnanthes*, having marginally disposed ovules (Fig. 123). Curiously, however, *Pyrrorhiza* (Fig. 125) and *Haemodorum* (Fig. 124), which possess two hypotropous ovules per carpel, have an enlarged placenta similar to that of *Lachnanthes* and *Schiekia*. In addition, an

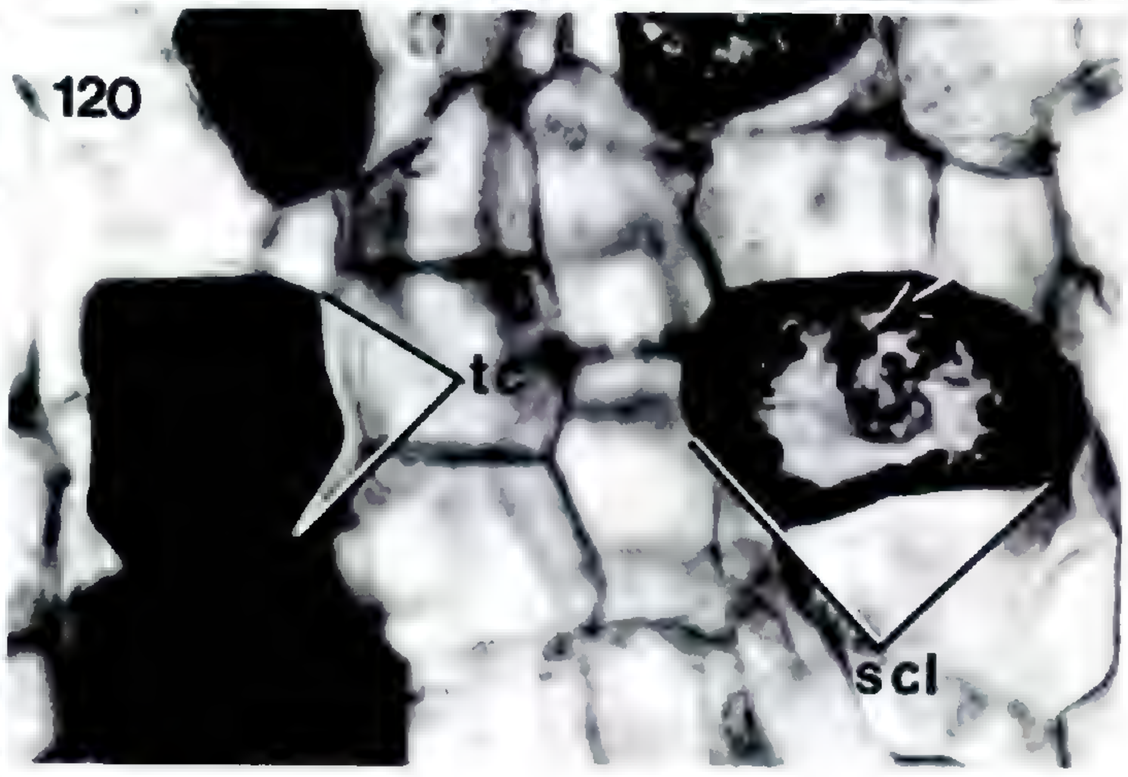




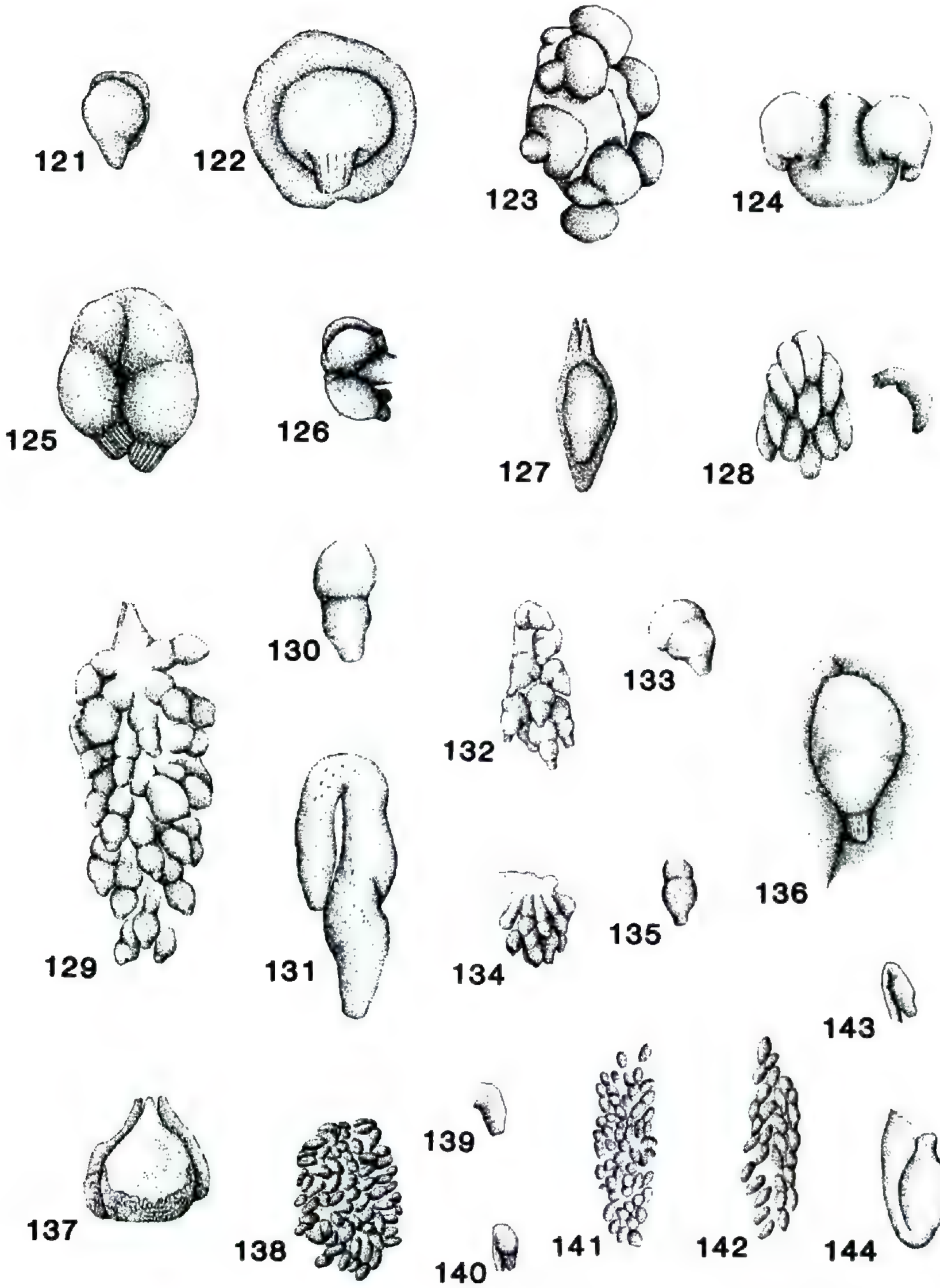








FIGURES 113–120. Placental tissue anatomy in the Haemodoraceae and outgroups. 113, 114. *Anigozanthos flavidus*.—113. Elongate sclereid (scl) with lignified cell wall; ×347.—114. Close-up of sclereid, showing nodulelike structures (arrow) appressed to inner cell wall; ×910.—115. *Tribonanthes variabilis*. Note lignified sclereid (scl) with nodulelike structures (arrow); ×856.—116. *Phlebocarya ciliata*. Note sclereid (scl) with nodules (arrow) and tannin cell (tc); ×856. 117–119. *Philydrum lanuginosum*.—117. Sclereid (scl) and tannin cell (tc); ×443.—118. Elongate sclereids with nodulelike structures (arrow); ×437.—119. Close-up of sclereid (scl), showing nodules (arrow); ×949.—120. *Pontederia cordata*. Note tannin cells (tc) and sclereid (scl) with nodules (arrow); ×887.



FIGURES 121–144. Ovule morphology in the Haemodoraceae and outgroups.—121. *Barberetta aurea*; ×19.—122. *Dilatris corymbosa*; ×19.—123. *Lachnanthes caroliniana*; ×19.—124. *Haemodorum spicatum*; ×19.—125. *Pyrrorhiza neblinae*; ×19.—126. *Schiekia orinocensis*; ×19.—127. *Wachendorfia thyrsiflora*; ×19.—128. *Xiphidium coeruleum*; ×19.—129, 130. *Anigozanthos flavidus*; ×9.5 (129), ×19 (130).—131. *Anigozanthos rubra*; ×19.—132, 133. *Blancoa canescens*; ×9.5 (132), ×19 (133).—134, 135. *Conostylis aurea*; ×9.5 (134), ×19 (135).—136. *Macropidia fuliginosa*; ×19.—137. *Phlebocarya ciliata*; ×19.—138, 139. *Tribonanthes variabilis*; ×9.5 (138), ×19 (139).—140, 141. *Helmholtzia acorifolia*; ×19 (140), ×9.5 (141).—142, 143. *Heteranthera reniformis*; ×9.5 (142), ×19 (143).—144. *Pontederia cordata*; ×19.

enlarged placenta consisting of a ringlike mass of tissue surrounding the base of the ovule is present in *Barberetta* (Fig. 121), *Dilatris* (Fig. 122), and *Wachendorfia* (Fig. 127). (In *Dilatris* this ring of tissue expands during seed development, forming a false aril; see De Vos, 1956.) It seems likely that the enlarged placentae of all seven of these genera are homologous; however, it is not immediately evident which morphology (i.e., the ringlike placenta surrounding a single ovule or the peltiform placenta bearing several marginal ovules) is most ancestral.

Among other OTUs, *Anigozanthos rubra* (Fig. 131) has two hypotropous ovules per carpel, and *Macropidia* (Fig. 136) has a single ovule per carpel. In both of these taxa, a distinct ringlike or enlarged placenta like that found in other Haemodoraceae is lacking; however, the inner ovary wall surrounding the ovule(s) is somewhat swollen and may be homologous to the enlarged placenta

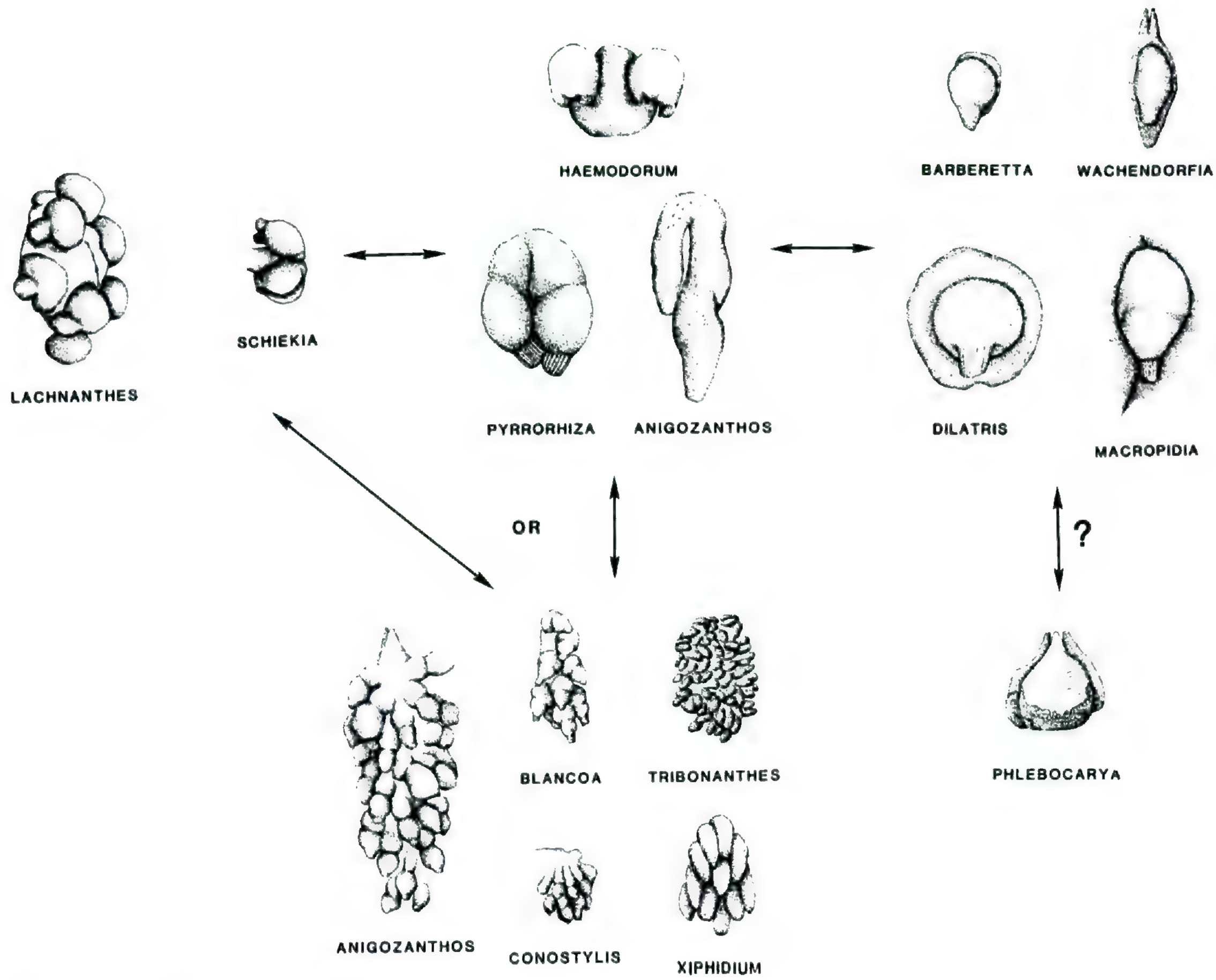


FIGURE 145. Hypothesized intergradation series of ovule types in the Haemodoraceae. Note uncertainty of evolutionary direction of single, epitropous ovule in *Phlebocarya*.

discussed above. Finally, numerous (up to 40) ovules per carpel are found in *Anigozanthos flavidus* (Figs. 129, 130), *Blancoa* (Figs. 132, 133), *Conostylis* (Figs. 134, 135), *Tribonanthes* (Figs. 138, 139), and *Xiphidium* (Fig. 128). Although the placentae in these taxa may be somewhat expanded (e.g., certain species of *Conostylis*), it appears unlikely that the greater ovule number in these taxa is directly related evolutionarily to that in *Schiekia* and *Lachnanthes*.

The possible evolutionary changes in ovule number, ovule morphology, and placenta morphology in the Haemodoraceae are rather complex. An unambiguous intergradation series is not evident. However, the morphocline presented in Figure 145 is presented as the most likely a priori hypothesis. Note that *Lachnanthes* and *Schiekia*, having 4–7 pleurotropous ovules/carpel, are coded either as derived from two-ovulate taxa *or* as intermediate between two-ovulate taxa and numerous-ovulate taxa. *Phlebocarya*, with one epitropous ovule/carpel, is questionably linked to taxa with one hypotropous ovule/carpel.

In order to code the character "ovule morphology and number" numerically without biasing the input, this feature was divided into the following four characters.

Characters #44, 45: Ovule position: PLEUROTROPOUS ←[#44]→ HYPOTROPOUS ←[#45]→ EPITROPOUS. Note that the epitropously positioned ovules of *Phlebocarya* are evolutionarily linked to the hypotropous condition (Fig. 145). Correspondingly, it seems quite unlikely that the specialized pleurotropous ovules arising from a peltiform placenta are evolutionarily intermediate to a hypotropous and epitropous condition (Fig. 145).

Character #46: Ovule number one per carpel vs. two–numerous per carpel. This character allows for a single evolutionary step between those taxa

with one ovule and those with two or more (see Figs. 145, 165C).

Character #47: Ovule number one or two per carpel vs. numerous per carpel. *Lachnanthes* and *Schiekia*, having (respectively) 4 and 5–7 ovules per carpel are coded as "X" so as to avoid bias for evolutionary linkage either directly with two-ovulate taxa or intermediate between two- and numerous-ovulate taxa (Fig. 165C). Figure 165C illustrates the character coding for ovule position and number (characters #44–47). Note that the number of steps between adjacent ovule groupings is one.

Among the outgroup families, all members of the Philydraceae have numerous ovules per carpel with a hypotropous to pleurotropous position (illustrated for *Helmholtzia* in Figs. 140, 141). However, in view of the distinctive placental morphology of those Haemodoraceae with pleurotropous ovules (i.e., positioned along the margin of a protruding placenta), the pleurotropous ovule position in the Philydraceae is not coded as being homologous with that in the Haemodoraceae. In the Pontederiaceae all genera have numerous, generally hypotropous ovules (illustrated for *Heteranthera* in Figs. 142, 143), with the exception of *Pontederia* (Fig. 144) and *Reussia*, which have one epitropous ovule per ovary (contained in the single fertile carpel). Thus, the Pontederiaceae are coded as polymorphic ("?") with respect to characters #45–47 (but not, of course, with respect to character #44).

Characters #48–50. Seed morphology. Seed morphology in the Haemodoraceae is quite variable. *Dilatris*, *Haemodorum*, and *Lachnanthes* have glabrous, discoid seeds (generally concave proximally and convex distally) which are peltately attached (i.e., the funiculus is positioned centrally on the proximal face). Various degrees of a marginal wing occur on the seeds of these taxa. Seeds of *Dilatris* (Fig. 146) are comparatively large (certainly correlated with having only one ovule per carpel) and have a narrow encircling wing. *Haemodorum* seeds (two per carpel) are slightly smaller and have a prominent marginal wing (Fig. 147). Seeds of *Lachnanthes* (5–7 per carpel) have only a slight marginal wing (Fig. 148), which develops from the growth and "buckling" of the outer integument (Simpson, 1988). Seeds of *Pyrrorhiza* (Figs. 149, 150) resemble those of the above three genera in being rather discoid and peltately attached but differ in having a dense tomentum of mostly marginal trichomes. *Wachendorfia* seeds range from globose (Fig. 154) to ovoid (Fig. 155) but are consistently pubescent to tomentose throughout. The individual trichomes of the seeds of *Wachendorfia* are quite similar to those of *Pyrrorhiza*; thus the seed morphology of *Pyrrorhiza* seems intermediate between that of *Wachendorfia* and the three genera with discoid glabrous seeds. Seeds of *Xiphidium* (Fig. 151) and *Schiekia* (Fig. 152) are globose and tuberculate. *Barberetta* (Fig. 153) has ovoid, glabrous seeds, which are very similar in size and shape to some species of *Wachendorfia*. *Phlebocarya* (Fig. 156) and *Tribonanthes* (Fig. 157) have glabrous and somewhat globose seeds. Seeds of *Anigozanthos* (Fig. 158), *Blancoa*, and *Conostylis* (Fig. 159) are quite similar to one another, being ellipsoid and ridged longitudinally. *Macropidia* (Fig. 160) has similar seeds to these three genera, but the ridges are much shallower and the seeds are significantly larger.

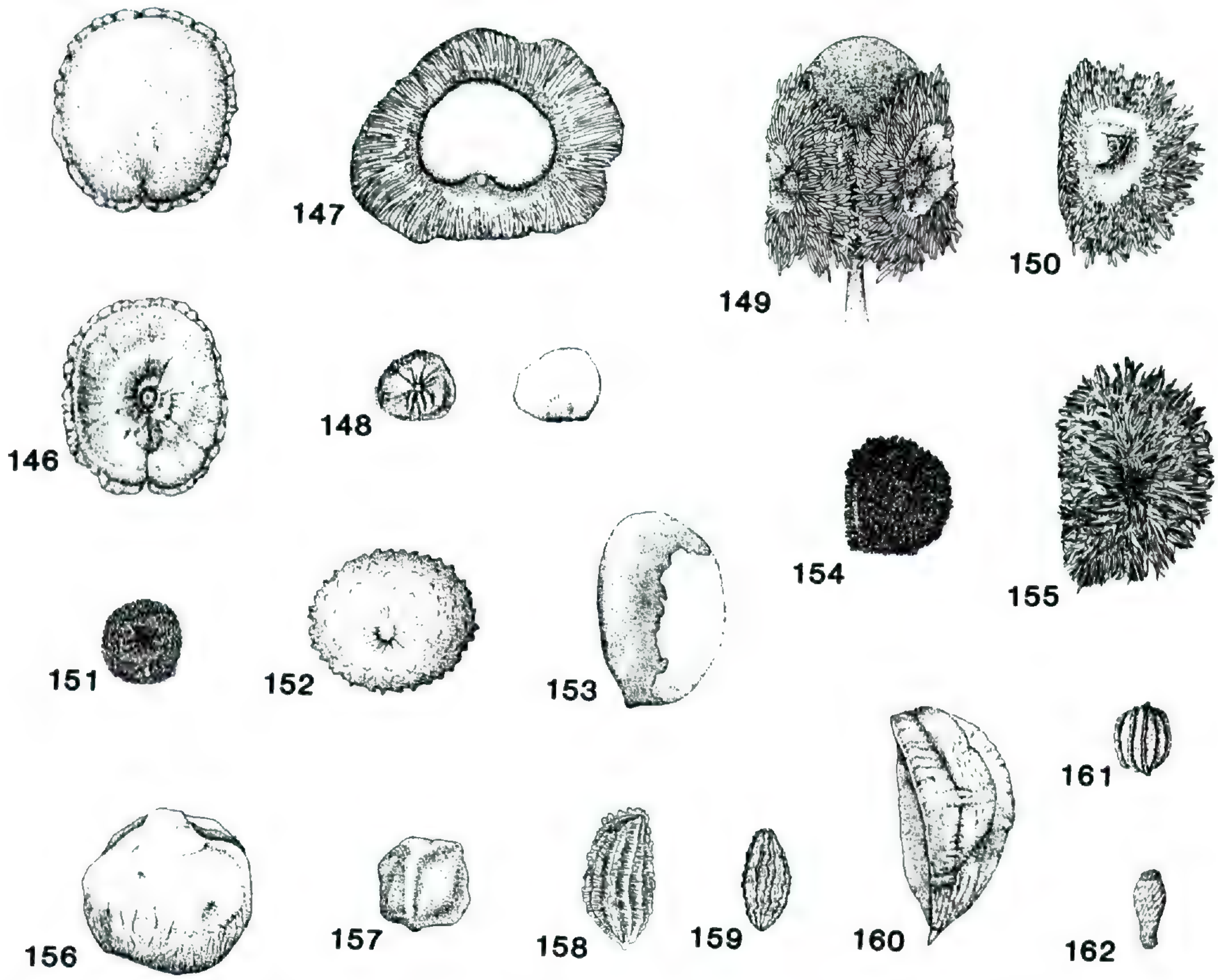
The hypothesized intergradation series for seed morphology in the Haemodoraceae is seen in Figure 163. Note that the direct evolutionary linkage between taxa with discoid, marginally winged seeds and the somewhat discoid, marginally tomentose seeds of *Pyrrorhiza* is questionable; developmental and anatomical studies are needed for confirmation. Because of the length of the morphocline of Figure 163 and the possibility of biasing the data if the groupings are coded sequentially, the character "seed morphology" was subdivided into the following discrete characters:

Character #48: Seed shape ovoid-globose or ellipsoid (and longitudinally ridged) vs. discoid. This allows for a single evolutionary step between taxa having the distinctive discoid seed morphology and all other taxa. *Pyrrorhiza* is coded as "X" for this character because of the uncertainty of homology between its somewhat flattened seeds and the discoid seeds of *Dilatris*, *Haemodorum*, and *Lachnanthes*.

Character #49: Seed shape ellipsoid vs. discoid, flattened, or ovoid-globose. This allows for a single evolutionary step between taxa having ellipsoid (and longitudinally ridged) seeds and all other seed types.

Character #50: Seed vestiture glabrous vs. pubescent or marginally winged. Taxa having discoid seeds with marginal wings are coded with those having tomentose seeds because of the presumed homology between the marginal wing and the trichomes. Figure 165D illustrates the character coding for seed morphology (characters #48–50).

Among the outgroups, seeds of all members of



FIGURES 146–162. Seed morphology in the Haemodoraceae and outgroups.—146. *Dilatris viscosa*, proximal (below) and distal (above) sides; ×3.8.—147. *Haemodorum spicatum*, distal side; ×3.8.—148. *Lachnanthes caroliniana*, proximal (left) and distal (right) sides; ×3.8. 149–150. *Pyrrorhiza neblinae*.—149. Face view of placenta with two attached seeds; ×3.8.—150. Proximal side of seed; ×3.8.—151. *Xiphidium coeruleum*, distal side; ×7.9.—152. *Schiekia orinocensis*, distal side; ×7.9.—153. *Barberetta aurea*, side view; ×7.9. 154–155. *Wachendorfia* seeds (side view).—154. *W. paniculata*; ×3.8.—155. *W. thyrsiflora*; ×3.8.—156. *Phlebocarya ciliata*; ×7.9.—157. *Tribonanthes variabilis*; ×7.9.—158. *Anigozanthos flavidus*; ×7.9.—159. *Conostylis* sp.; ×7.9.—160. *Macropidia fuliginosa*; ×7.9.—161. *Eichhornia* sp.; ×7.9.—162. *Philydrum lanuginosum*; ×7.9.

the Pontederiaceae (see Fig. 161) are consistently small and ovoid with longitudinal ridges. Species of the Philydraceae (see Fig. 162) have twisted, pyriform-terete seeds with longitudinal rows of epidermal cells. Thus the seeds of both outgroups, particularly the Pontederiaceae, resemble *Anigozanthos*, *Blancoa*, *Conostylis*, and *Macropidia* in having longitudinal ridges but differ somewhat in shape. Because of the similarity, seed morphology in the Philydraceae and Pontederiaceae are coded as homologous with the ellipsoid, longitudinally ridged seeds in the Haemodoraceae.

Character #51. Haploid chromosome number. Haploid chromosome numbers for the Haemodoraceae and outgroups are listed in Table 6. The chromosome number of *Xiphidium coeruleum* is here described for the first time as $n = 19$ (Fig. 164; this number confirmed by P. Goldblatt of the Missouri Botanical Garden, pers. comm.). Note that chromosome numbers of *Pyrrorhiza* and *Schiekia* are unknown. Of the genera in the Haemodoraceae, only *Conostylis* has a variable number. However, most species of that genus have a count of $n = 8$, and the exemplar OTUs are either $n = 5$ or $n = 8$.

One possible coding for chromosome number is the arrangement of taxa in classes via a linear morphocline, such as: $n = 5–8 \leftrightarrow n = 15 \leftrightarrow n = 19–21 \leftrightarrow n = 24$. (Chromosome numbers ranging from 5 to 8 in the OTUs are lumped into one class because of the difficulty of assessing evolutionary direction in presumed minor aneuploidy events.) Since nothing in the Haemodoraceae is known regarding karyological details, it is not unlikely that the evolution of chromosome number may have occurred differently from the simple numerical sequence listed above. For example, the fact that *Lachnanthes* ($n = 24$) has a chromosome number

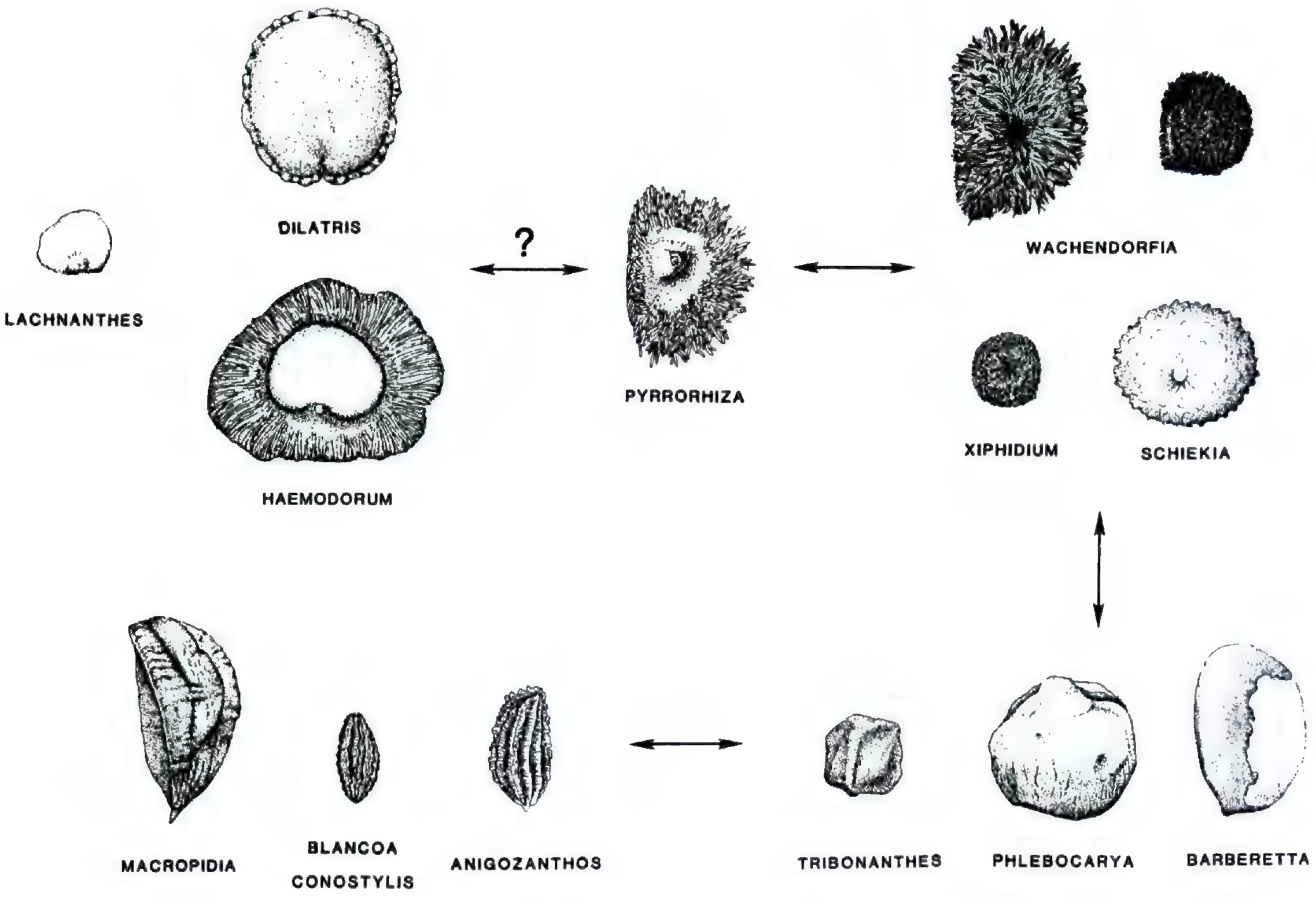


FIGURE 163. Hypothesized intergradation series of seed types in the Haemodoraceae.

exactly 3 times that of the most common number ($n = 8$) may be evidence of a hexaploid derivation from an ancestral $n = 8$; alternatively, a count of $n = 24$ may have arisen from an allopolyploidy event. The $n = 15$ count of some taxa may have been derived via a tetraploidy event, e.g., from an ancestral $n = 7$ or $n = 8$, followed by aneuploidy. A count of $n = 19$ could have arisen directly from a number of $n = 5$–8 or from an immediate ancestor having either $n = 15$ or $n = 24$.

After considerable experimentation with this character, it was concluded that the best coding is simply: $n = 5$–$8 \leftrightarrow n = 15$, 19–21, or 24. The transformation series between the higher haploid numbers is ambiguous, and more elaborate and complex coding schemes result in the same topology in the cladistic analysis.

Chromosome counts in the outgroups vary considerably (Table 6) and are consequently coded as polymorphic ("?"). The only haploid chromosome number found in both outgroups and in the Haemodoraceae is a count of $n = 8$. It seems most likely that the ancestral haploid chromosome number for the Haemodoraceae is near $n = 8$, a hypothesis to be tested with the cladistic analysis.

Character #52. Phenalenones absent vs. present. This character is included to establish the monophyly of the Haemodoraceae relative to the two outgroups (see Monophylesis of the Haemodoraceae). It is very likely that all species of the Haemodoraceae, if investigated, would be found to have these compounds. As a reasonable compromise, however, *genera* of the Haemodoraceae not yet chemically investigated are coded as unknown ("?"). If any species of a genus has been found to have the compounds, *all* species of that genus are coded as possessing them. Both outgroup families are coded as lacking phenalenones.

Character #53. Tapetum glandular vs. amoeboid. This character is included to consider the presence of an amoeboid tapetum in the Haemodoraceae and Pontederiaceae as a possible synapomorphy (see Outgroup Taxa, Table 5). As above, genera of the Haemodoraceae not yet investigated for this feature are coded as unknown ("?"). If any species of a genus has been found to have an amoeboid tapetum, *all* species of that genus are coded as having it.

Character #54. Pollen exine wall structure tetacte-columellate vs. non-tectate-columellate. This feature is included to denote the evidence discussed earlier that the Pontederiaceae are the sister group to the Haemodoraceae (see Out-

TABLE 6. Chromosome numbers in the Haemodoraceae and related families.

Taxon	$2n =$	$n =$	Citation
Tribe Haemodoreae			
Barberetta aurea Harv.		15	Hilliard & Burtt (1971); Ratter & Milne (1973); Ornduff (1979a)
Dilatris pilansii Barker		ca. 19–21	Ornduff (1979a)
Haemodorum sp.		8	G. Keighery (pers. comm.)
Lachnanthes caroliniana (Lam.) Dandy		24	Ornduff (1979a)
Lanaria lanata (L.) Dur. & Schinz		36	Ornduff (1979a)
Lophiola aurea Ker-Gawler		21	Ornduff (1979a)
Phlebocarya			
ciliata R. Br.		7	*G. Keighery 691* (PERTH)
filifolia F. Muell.		7	*S. Hopper 840* (PERTH)
Wachendorfia			
paniculata L.		15	Ornduff (1979a)
thyrsiflora L.		ca. 15	Ornduff (1979a)
Xiphidium coeruleum Aubl.		19	Simpson (present paper); P. Goldblatt (pers. comm.)
Tribe Conostylideae			
Anigozanthos			
bicolor Endl.		6	Green (1961)
flavidus DC.		6	Stenar (1927); Green (1961)
humilis Lindl.		6	Green (1961)
manglesii D. Don		6	Green (1961)
viridis Endl.		6	Green (1961)
Blancoa canescens Lindl.		8	Green (1961)
Conostylis			
aculeata R. Br. (7 subspecies)		8	Green (1961); Hopper (1978)
androstemma F. Muell.		5	Green (1961)
aurea Lindl.		5	Green (1961)
bealiana F. Muell.		8	Green (1961)
breviscapa R. Br.		4	Green (1961)
candicans Endl.		8	Green (1961)
caricina Lindl.		7	Green (1961)
filifolia F. Muell.		8	Green (1961)
juncea Endl.		8	Green (1961)
phathyrantha Diels		8	Green (1961)
seorsiflora F. Muell.		8	Green (1961)
serrulata R. Br.		8	Green (1961)
setigera R. Br.		14	Green (1961)
setosa Lindl.		7	Green (1961)
stylidioides F. Muell.		8	Green (1961)
stylidioides F. Muell.		16	Hopper (1978)
vaginata Endl.		8	Green (1961)
Macropidia fuliginosa (Hook.) Druce		6	Green (1961)
Tribonanthes sp.		7	G. Keighery (pers. comm.)
Apostasiaceae (no counts reported)			
Hypoxidaceae			
Curculigo			
orchioides Gaertn.	36		Sharma & Ghosh (1954); Sharma & Chaudhuri (1964); Mitra (1966)
orchioides Gaertn.	18		Raghavan (1957); Sharma & Bhattacharyya (1960)

TABLE 6. Continued.

Taxon	$2n =$	$n =$	Citation
recurvata Dryand.	18		Sharma & Ghosh (1954); Sharma & Chaudhuri (1964)
Hypoxis			
acuminata		18, 20	Wilsenach & Papenfus (1967)
aurea Lour.	54		Mehra & Sachdeva (1971, 1976)
decumbens L.	42		Naranjo (1975)
filiformis		7	Wilsenach & Papenfus (1967)
longifolia Baker	72		Wilsenach (1967)
multiceps Buchinge	36		Wilsenach (1967)
nitida		ca. 40–42	Wilsenach (1967)
pusilla Hook.f.	28		Beuzenberg & Hair (1963)
rooperi	96	ca. 43–58	Wilsenach & Papenfus (1967); Wilsenach (1967)
rooperi Moore	76, 114	18	Fernandez & Neves (1962)
stellipilis (Ker.)	16		Fernandez & Neves (1962)
zeyheri Baker (?)	32		Fernandez & Neves (1962)
Rhodohypoxis			
baueri Nel. (9 cultivars)	18, 12		Saito (1975)
Philydraceae			
Helmholtzia			
acorifolia F. Muell.	34		Briggs (1966)
glaberrima (Hook.f.) Caruel	34		Briggs (1966)
Orthothylax			
glaberrimus		16	Hamann (1966)
Philydrum			
langinosum Banks & Soland.	16	8	Hamann (1966) Briggs (1966)
Pontederiaceae			
Eichhornia			
crassipes (Mart.) Solms	36		Briggs (1966)
crassipes Solms	32		Krishnappa (1971)
crassipes Solms	30, 32, 58	16	Banerjee (1974)
speciosa Kunth		8	Sarkar et al. (1975)
Monochoria			
hastifolia Presl.	28, 34–84	14, 40, 42	Banerjee (1974)
korsakowii Rgl.	52		Sokolovskaya (1966)
vaginalis	28		Hsu (1967)
vaginalis	26, 52, 72, 74, 80	30, 40	Sharma (1970)
vaginalis Presl ex Kunth	52		Krishnappa (1971)
vaginalis Presl	80	40	Sharma & Sarkar (1967–1968)
vaginalis Pax. var. *plumbaginia* Solms-Laubch.	52		Sharma & Sarkar (1967–1968)
vaginalis Presl var. *plumbaginea* Solms-Laubch.	52		Banerjee (1974)
vaginalis Presl var. *plumbaginea* Solms-Laubch.	52		Sharma (1970)
vaginalis (L.) Presl	80	40	Sharma (1970)
vaginalis (L.) Presl	52		Mehra & Pandita (1978)
Pontederia			
cordata L.		8	Ornduff (1969); Lowden (1973)
parviflora Alex.		8	Lowden (1973)
rotundifolia L.f.		16	Lowden (1973)
sagitta Presl		8	Lowden (1973)
Tecophilaeaceae			
Cyanastrum			
cordifolium L.	22		Sato (1942)

TABLE 6. Continued.

Taxon	$2n =$	$n =$	Citation
cordifolium L.		12	Nietsch (1941)
Cyanella			
abla L.f.		12	Ornduff (1979b)
hyacinthoides L.		12, 14, 24	Ornduff (1979b)
lutea L.f. var. *lutea*		8, 12, 24	Ornduff (1979b)
lutea L.f. var. *rosea* Bak.		12	Ornduff (1979b)
orchidiformis Jacq.		12	Ornduff (1979b)
Odontostomum			
hartwegii Torr.		10, 10 + f	Cave (1970)
Tecophilaea			
cyano-crocus		12	LaCour (1956)
Velloziaceae (no counts reported)			
Walleriaceae (*Walleria* spp.)	24		Goldblatt (1989)

group Taxa; Simpson, 1987). Thus, all Pontederiaceae are coded similarly to all Haemodoraceae as having a non-tectate-columellate architecture. Note that this feature was not taken into account with respect to the early characters (#33–37) "exine wall structure," as the Philydraceae were coded as ("?") for number of exine layers (characters #33, 34).

Character #55. Leaves unifacial vs. bifacial. All Haemodoraceae and all Philydraceae have unifacial leaves, whereas all Pontederiaceae have bifacial leaves. This character is included to take into account what may represent a shared derived feature between the Haemodoraceae and Philydraceae.

CLADISTIC ANALYSIS

METHODS

Cladistic analyses were implemented using PAUP (Phylogenetic Analysis Using Parsimony), version 2.4 (Swofford, 1983), on an IBM-AT compatible microcomputer. The most parsimonious trees were constructed using the "branch and bound" algorithm from the data matrix of Table 8. Wagner parsimony was used throughout. Coding is summarized in Table 7. (See Conclusions for results of recent analyses using unordered character coding.)

In the initial analysis all characters were assigned equal weight. In a subsequent analysis characters that could originally have been treated as states of a single character (e.g., characters #4–6, all dealing with inflorescence type) were "scaled," weighted as a proportional fraction of their original weight of "1" (characters #4, 5, and 6 were each given a weight of ⅓). This takes into account (often unintentional) a priori weighting of a feature because it can be subdivided into two or more correlated binary characters. The following characters were fractionally weighted in this second analysis: #4–6, 7–13, 15, 16, 21, 22, 23–25, 27, 28, 29, 30, 33–37, 44–47, 48–50, and 51–53.

In a third cladistic analysis, only those characters for which the polarity could be determined at the outgroup node, using the method of Maddison et al. (1984), were included. Thus, the following eleven characters, for which polarity could not be determined at the outgroup node, were omitted from this analysis: characters #4, 17, 23, 24, 25, 33, 35, 36, 53, 54, and 55.

RESULTS AND DISCUSSION

For the complete data set of Table 8, there are two equally most parsimonious cladograms (Figs. 166, 167). The consistency index of the global analysis, including both outgroups, is 55/88 = 0.625. (If the 10 characters which are nonhomoplasious and autapomorphic for OTUs of the Haemodoraceae are deleted, the consistency index is 45/78 = 0.577.) When "fractional weighting" was performed (see Methods), a single most parsimonious cladogram was computed, equivalent to that of Figure 166. Thus, it could be argued that coding several characters in a multistate transformation series results in little change in cladistic relationships. When the characters for which polarity could not be determined were omitted from the data set, the same two cladograms of Figures 166 and 167 were obtained. This confirmation of results is important because, with some data sets, inclusion versus omission of nonpolarized characters may yield significantly different cladistic re-

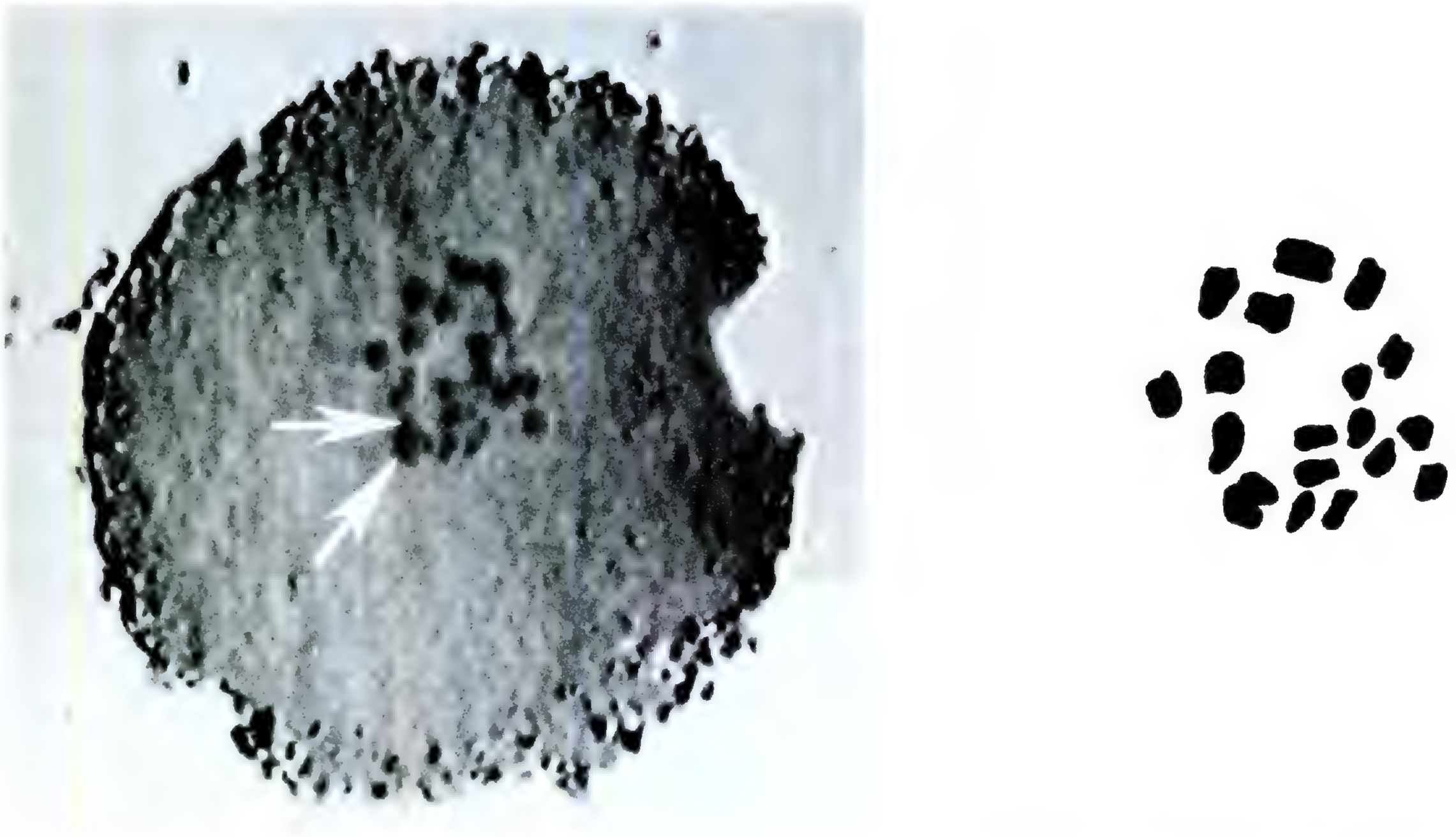


FIGURE 164. Anther microsporocyte squash of *Xiphidium coeruleum* at metaphase I. Note 19 bivalents. Arrows point to overlapping, but different, bivalents. ×1,750 (left), ×2,770 (right).

lationships. (Further comparison of alternative cladograms to Figures 166 and 167 will be discussed below.)

As discussed earlier, the two outgroups were treated as OTUs equivalent in treatment to the intrafamilial OTUs of the Haemodoraceae. Because the outgroup relationships were not coded as resolved, this cladistic analysis confirms the Haemodoraceae as monophyletic; i.e., all OTUs of the ingroup are more closely related to one another than to either outgroup. The overall tree was rooted at the Philydraceae clade, based on assumptions of polarity of characters #52–55 (Table 8; see Fig. 176). The alternative methodology of assigning a hypothetical ancestor and determining the states of that ancestor via the "2-step" algorithm of Maddison et al. (1984) would have yielded identical results within the Haemodoraceae. However, one possible advantage of this "1-step" analysis (sensu Maddison et al.), performed *without* specifying outgroup relationships, is that it provides a test both for the monophyly of the ingroup and for the relationship of the ingroup to the outgroup (see Interfamilial Relationships).

Synapomorphies for the Haemodoraceae (Fig. 166) are: bifurcate cymes (character #5); inferior ovary position (character #39); discoid, flattened, or ovoid-globose, i.e., *not* ellipsoid and ridged, seeds (character #49); and presence of phenalenone compounds (character #52). Of these, only the presence of phenalenone compounds was hypothesized a priori as synapomorphic for the family (see Monophylesis of the Haemodoraceae). Corroboration here confirms its valid use as a synapomorphy for the family. (The indicated occurrence of bifurcate cymes, inferior ovary position, and nonellipsoid, ridged seeds as synapomorphies for the Haemodoraceae is discussed below.)

The two equally parsimonious topologies differ only in the relationship of *Dilatris*, portrayed either as the sister taxon of *Lachnanthes* alone (Fig. 166) or as the sister taxon of the monophyletic group containing SC-PY-XI-BA-WA (Fig. 167). In either topology it is interesting that the initial bifurcation defines two monophyletic groups: designated here tribe Haemodoreae and Conostylideae. These roughly correspond to the traditionally defined tribes Haemodoreae and Conostylideae (e.g., Bentham & Hooker, 1883; Hutchinson, 1973; Melchior, 1964; Geerinck, 1969a) or the subfamilies Haemodoroideae and Conostyloideae (Cronquist, 1981; Dahlgren & Clifford, 1982). Thus, the present analysis confirms the taxonomic "integrity" of tribes Conostylideae and Haemodoreae and provides evidence for their being monophyletic taxa. (Despite the many differences in significant patristic distance between these two major clades of the Haemodoraceae, I conform with historical priority and recent consensus of use in retaining the tribal rather than the subfamilial rank. I see no valid reason for

TABLE 7. Character listing and coding. Originally multistate characters were recoded as two or more binary characters.

1. Reddish root and stem coloration
   0 = absent
   1 = present
2. Stem structural type
   0 = rhizome
   1 = corm
3. Plicate leaves
   0 = absent
   1 = present
4. Inflorescence type
   0 = cyme absent
   1 = cyme simple, bifurcate, or trifurcate
5. Inflorescence type
   0 = cyme absent or simple
   1 = cyme bifurcate or bifurcate and trifurcate
6. Inflorescence type
   0 = cyme absent, simple, or bifurcate
   1 = cyme bifurcate and trifurcate
7. Trichomes pilate
   0 = absent
   1 = present
   ? = homology uncertain
8. Trichomes, if pilate, with basal rosette
   0 = absent
   1 = present
   ? = not pilate
9. Trichomes tapering
   0 = absent
   1 = present
10. Trichomes, if tapering, unicellular or multicellular
   0 = unicellular
   1 = multicellular
   ? = nontapering
11. Trichomes, if tapering, uniseriate or multiseriate
   0 = uniseriate
   1 = multiseriate
   ? = nontapering
12. Trichomes, if tapering, branched
   0 = absent (unbranched)
   1 = present (branched)
   ? = nontapering
13. Trichomes, if tapering, with basal rosette
   0 = absent
   1 = present
   ? = nontapering
14. Perianth apertures
   0 = absent
   1 = present
15. Perianth tube
   0 = absent
   1 = present (short or long)
16. Perianth tube
   0 = absent or short
   1 = long
17. Perianth symmetry
   0 = actinomorphic
   1 = zygomorphic (without perianth splitting)
18. Perianth splitting
   0 = absent
   1 = present
19. Perianth aestivation
   0 = imbricate
   1 = valvate
20. Perianth tannin cells
   0 = absent
   1 = present
21. Stamen (fertile) number
   0 = six
   1 = three or one
22. Stamen (fertile) number
   0 = six or three stamens + two latero-anterior staminodes
   1 = three (without staminodes) or one
23. Anther dimorphism
   0 = anthers equal
   1 = anthers dimorphic
24. Anther dimorphism
   0 = anthers equal *or* one large + two small anthers
   1 = one large + two caducous anthers *or* one anther + two staminodes
25. Anther dimorphism
   0 = anthers equal *or* one large + two small or caducous anthers
   1 = one anther + two staminodes
26. Stamen connective appendages
   0 = absent
   1 = present
27. Pollen aperture
   0 = monosulcate
   1 = porate
28. Pollen aperture
   0 = monosulcate or 2–3-porate
   1 = oligoforaminate
29. Pollen sculpturing
   0 = foveolate
   1 = verrucate or rugulate
30. Pollen sculpturing
   0 = foveolate or verrucate
   1 = rugulate
31. Pollen apertural border
   0 = absent
   1 = present
32. Pollen large proximal verrucae
   0 = absent
   1 = present
33. Number of exine wall layers
   0 = one-layered
   1 = two- or three-layered
34. Number of exine wall layers
   0 = one- or two-layered
   1 = three-layered
35. Exine wall, if two-layered, with papillate inner elements
   0 = absent

TABLE 7. Continued.

1 = present
? = exine one- or three-layered
36. Exine wall, if two-layered, with only papillate inner elements
0 = absent
1 = present
? = exine one- or three-layered
37. Subexterior exine wall discontinuous
0 = absent
1 = present
38. Enantiostyly
0 = absent
1 = present
39. Ovary position
0 = superior
1 = inferior
40. Septal nectaries
0 = absent
1 = present
41. Fertile carpels
0 = three
1 = one
42. Locule number
0 = three
1 = one
43. Placental sclereids
0 = absent
1 = present
44. Ovule position
0 = pleurotropous
1 = hypotropous or epitropous
45. Ovule position
0 = pleurotropous or hypotropous
1 = epitropous
46. Ovule number
0 = one per carpel
1 = two–numerous per carpel
47. Ovule number
0 = one or two per carpel
1 = numerous per carpel
? = four–seven per carpel
48. Seed shape
0 = ovoid-globose *or* ellipsoid (& longitudinally ridged)
1 = discoid
? = flattened (*Pyrrorhiza*)
49. Seed shape
0 = ellipsoid (& longitudinally ridged)
1 = discoid, flattened, or ovoid-globose
50. Seed vestiture
0 = glabrous
1 = pubescent or marginally winged
51. Haploid chromosome number
0 = 5–8
1 = 15, 19–21, or 24
? = unknown or polymorphic
52. Presence of phenalenone compounds
0 = absent
1 = present
? = unknown
53. Tapetum type
0 = secretory
1 = amoeboid
? = unknown
54. Exine structure
0 = tecate-columellate
1 = non-tectate-columellate
55. Leaf type
0 = bifacial
1 = unifacial

promoting a change in rank that conveys no change in cladistic relationships.)

The present circumscription of the tribes differs from past treatments primarily in the removal of *Hagenbachia*, *Lanaria*, *Lophiola*, and *Pauridia* from the family and in the transfer of *Phlebocarya* from its usual placement in the tribe Haemodoreae to the Conostylideae. *Phlebocarya* has traditionally been placed in the tribe Haemodoreae because of its imbricate as opposed to valvate tepals. However, an imbricate perianth is clearly plesiomorphic for members of the family; its occurrence cannot be used to unite taxa in a phylogenetic classification. *Phlebocarya* is united with the other Conostylideae by the common occurrence of derived features (see below).

Synapomorphies shared by the six genera of the Conostyloideae are: loss of pilate trichomes (character #7, although this may be synapomorphic only for members of the tribe other than *Phlebocarya*; see Fig. 166), possession of multiseriate trichomes (character #11, which has an alternative state change possibility; see below), branched trichomes (character #12), six fertile stamens (character #21), six or three stamens + two latero-anterior staminodes (character #22), porate apertures (character #27), rugulate pollen wall sculpturing (character #30), and absence of enantiostyly (character #38). Character #11 exhibits a reversal in the clade to *Tribonanthes* (Fig. 166); an equally parsimonious alternative (but highly unlikely in the author's view) is the independent evolution of multiseriate trichomes in the clades to *Phlebocarya* and to the COau–MA monophyletic group. Of the other indicated synapomorphies, it seems extremely likely that the palynological fea-

TABLE 8. Character × Taxon matrix for the Haemodoraceae. A "?" indicates uncertain ancestry, absent data or "X" coding. (See Table 7 and text for discussion of taxa and character coding.) PHIL = Philydraceae, PONT = Pontederiaceae. Other taxa abbreviations are listed in Figure 166.

	Characters:										
Taxa:	00000 12345	00001 67890	11111 12345	11112 67890	22222 12345	22223 67890	33333 12345	33334 67890	44444 12345	44445 67890	55555 12345
PHIL	0?000	01011	00000	0?001	11???	000??	00???	??100	1?110	11000	?0001
PONT	00010	01011	0000?	??001	?????	00010	00?0?	?0?0?	?011?	??000	?0110
ANfl	00011	00?11	11001	10110	00000	01011	00101	10011	00110	11000	01111
ANru	00011	00?11	11001	10110	00000	01011	00101	10011	00110	10000	01111
BA	00100	0110?	???00	00000	11000	00010	11100	00101	10010	00010	1??11
BL	00011	00?11	11001	10010	00000	01011	00101	10011	00110	11000	01?11
COan	00011	00?11	11001	10010	00000	01011	00101	10011	00110	11000	0??11
COau	00011	00?11	11001	00010	00000	01011	00101	10011	00110	11000	0??11
CObe	00011	00?11	11001	10010	00000	01011	00101	10011	00110	11000	0??11
DI	10011	11111	00100	00000	11100	00010	10100	00111	00010	00111	1?111
HA	11011	0100?	???00	00001	11100	00010	0000?	?0111	00010	10111	01?11
LA	10011	1?111	00000	00000	11000	00010	0000?	?0111	00000	1?111	11111
MA	00011	00?11	11001	10110	00000	01011	00101	10011	00110	00000	0??11
PH	00011	0??11	11000	00001	00000	01011	00101	00011	01111	00010	0??11
PY	11011	01110	00100	01000	11111	00010	00100	01001	00010	10?11	???11
SC	00011	01110	00110	01000	10110	00000	0011?	?1101	00000	1?011	???11
TR	01011	00?11	01001	00011	00000	11111	00101	10011	00110	11010	0??11
WA	11110	01110	00110	01000	11000	00010	11100	00101	00010	00011	11111
XI	10010	0110?	???00	00000	11100	00010	00100	00100	00010	11011	11111

tures are indeed synapomorphic, as supported by pollen investigations of all taxa considered closely related to the Haemodoraceae.

Within the tribe Conostylideae, *Phlebocarya* is the most basal taxon (Fig. 166). Characters shared by *Tribonanthes* and the remaining four genera (CO, BL, AN, & MA) are a short perianth tube (character #15), valvate perianth aestivation (character #19), inner exine layer composed solely of papillate elements (character #36), and numerous ovules per carpel (character #47). The last-mentioned feature (#47) requires a convergence (clade to XI) and a reversal (clade to ANru & MA). The placements of *Phlebocarya* and *Tribonanthes* are questionable. They are similar to one another in chromosome number ($n = 7$; see below), but no coded features argue for their being sister taxa. *Phlebocarya* shares two similarities with CO, BL, AN, & MA that *Tribonanthes* does not: presence of 2–3-porate pollen grains (character #27) and of multiseriate, dendritic trichomes (character #10). The occurrence of 2–3-porate pollen grains, however, is undoubtedly plesiomorphic for the tribe (Fig. 166), and *Tribonanthes* is presumed to have evolved this feature in common with other members of the tribe.

Conostylis, *Blancoa*, *Anigozanthos*, and *Macropidia* are members of a monophyletic group that is defined by two homoplasious synapomorphies: absence of perianth tannin cells (character #20 C) and presence of ellipsoid, longitudinally ridged seeds (character #49 R). All four of these genera have protruding hemispheric aperture walls (not found in *Phlebocarya* or *Tribonanthes*), which may represent a unique evolutionary change and thus constitute further evidence for the monophyly of these four genera. *Conostylis* and *Anigozanthos* are paraphyletic in the present analysis (Fig. 166). In *Conostylis* two exemplar species, COan & CObe, share more recent common ancestry with BL, AN, and MA than with COau as shown by the common presence of an elongate perianth tube (character #16), a derived feature. *Anigozanthos* and *Macropidia* clearly form a monophyletic group, as supported by their common possession of a unique longitudinal perianth splitting (character #18). However, *Anigozanthos* is portrayed as paraphyletic because MA and ANru share a derived feature: reduction of ovule number from numerous to one or two per carpel (character #47 R), a feature not shared with ANfl, which has numerous ovules per carpel.

The present study tends to support Geerinck's (1969a, b, 1970), treatment of *Macropidia* as a species of *Anigozanthos* (*A. fuliginosus*) and *Blancoa* as a species of *Conostylis* (*C. canescens*).

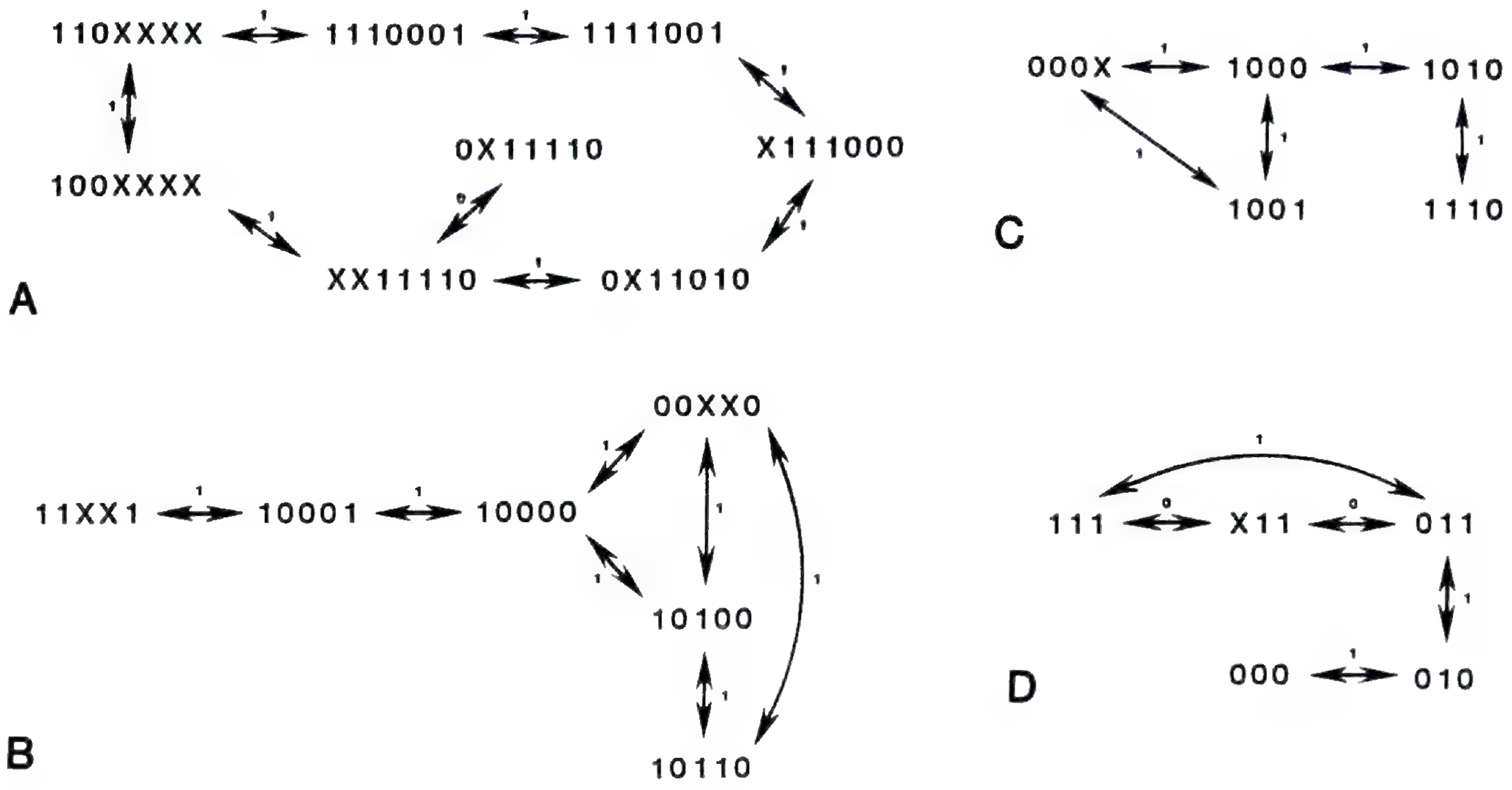


FIGURE 165. "X"-character state coding of OTUs of Haemodoraceae. Sequence of numbers and Xs represent character states of related characters for a given taxon. The "X" symbol represents an equivocal character state coding (coded as a "?" in Tables 7 and 8). Arrows represent evolutionary transitions in the morphocline. Numbers of character state changes are indicated beside arrows.—A. Trichome anatomy (characters #7–13), reflecting morphocline of Figure 28.—B. Pollen exine wall structure (characters #33–37), reflecting morphocline of Figure 112.—C. Ovule morphology (characters #44–47), reflecting morphocline of Figure 145.—D. Seed morphology (characters #48–50), reflecting morphocline of Figure 163.

Following Geerinck's treatment and accepting the results here, *Anigozanthos* s. ampl. would then be monophyletic. On the other hand, *Conostylis*, as currently defined, is still likely paraphyletic, even when merged with *Blancoa*. Much more detailed phylogenetic studies are needed to resolve the phylogenetic relationships of *Anigozanthos* and *Conostylis*, particularly in the recognition of genera segregated from *Conostylis*: *Blancoa*, *Greenia*, and *Androstemma* (see Keighery, 1981). Hopper & Campbell (1977), in study of seed morphology of *Anigozanthos* and *Macropidia*, attained results markedly different from those portrayed in Figure 166. Their phylogenetic tree suggests that *Anigozanthos* is a monophyletic group, and that the lineages to both *Anigozanthos* and *Macropidia* were derived separately from an ancestral taxon most closely related to the extant *Conostylis breviscapa*, the only species of *Conostylis* with distinct tepals. It is my view that *Anigozanthos* and *Macropidia* are likely most closely related to the long-tubular species of *Conostylis*, namely *C. bealiana*, *C. androstemma*, and/or *C.* (*Blancoa*) *canescens*. Clearly, however, a thorough character analysis and phylogenetic study of all species of this complex of taxa is needed.

Characters that unite the genera of the Haemodoreae are: reddish coloration in roots and rootstock (character #1), absence of placental sclereids (character #43), discoid seed shape (character #48, which has an alternative state change possibility; see below), and pubescent or marginally winged seed (character #50). Of these, only character #43 is nonhomoplasious and exhibits no reversals. Character #48 has an equally parsimonious alternative of two convergent events (in the clades to HA and to DI-LA). Additionally, note that characters #23 & #35 may be synapomorphic for *either* of the tribes Haemodoreae or Conostylideae, the uncertainty resulting from the fact that the polarity of these characters at the ingroup node (i.e., the common ancestor of the Haemodoraceae) could not be determined.

Within the tribe Haemodoreae, *Haemodorum* is the most basal (earliest diverging) lineage. The seven other genera of the tribe are united by four synapomorphies (see Fig. 166). Two of these, presence of pilate trichomes with a basal rosette of epidermal cells (character #8) and an increase in chromosome number from $n = 5–8$ to $n = 15–24$ (character #51), are nonhomoplasious in both equally parsimonious topologies and seem good evidence for the recognition of this subgroup. Absence (loss) of perianth tannin cells (character #20 C) occurs independently as a derived feature in the lineage to CO, BL, AN, and MA of the tribe Cono-

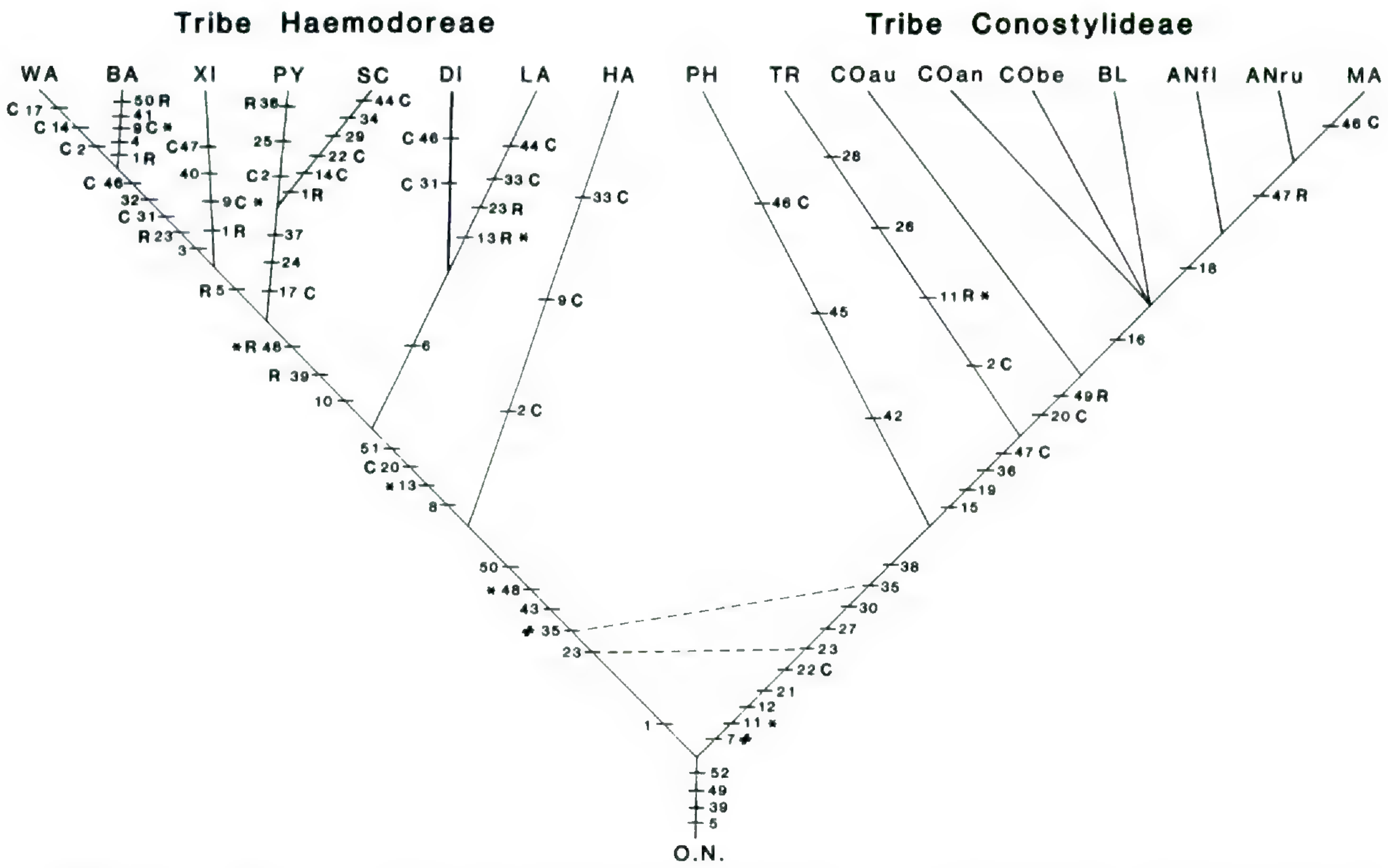


FIGURE 166. One of two equally most parsimonious cladograms of the Haemodoraceae derived from the data matrix of Table 8. Each numbered hash mark along a clade represents an apomorphic character state change of the designated character (Tables 7, 8). Dashed lines between character changes at base of cladogram represent equally parsimonious alternatives of evolutionary change along the lineages to either the tribe Haemodoreae or Conostylideae. Character state changes indicated with a "*" (characters 9, 11, 13, and 48) have two equally parsimonious alternatives, either two convergent events or one apomorphy and one reversal; only one of these alternatives (the most likely in the author's view) is displayed in the cladogram. State changes indicated with a "#" (characters 7 and 35) may occur with equal probability at the *internode* immediately above the displayed position.

Taxa abbreviations: O.N. = outgroup node; ANfl = *Anigozanthos flavidus*, ANru = *Anigozanthos rufus*, BA = *Barberetta aurea*, BL = *Blancoa canescens*, COau = *Conostylis aurea*, COan = *Conostylis androstemma*, CObe = *Conostylis bealiana*, DI = *Dilatris* spp., HA = *Haemodorum spicatum*, LA = *Lachnanthes caroliniana*, MA = *Macropidia fuliginosa*, PH = *Phlebocarya* spp., PY = *Pyrrorhiza neblinae*, SC = *Schiekia orinocensis*, TR = *Tribonanthes* spp., WA = *Wachendorfia thyrsiflora*, XI = *Xiphidium coeruleum*. C = Convergence; R = Reversal.

stylideae. The occurrence of tapering trichomes having a basal rosette of epidermal cells (character #13) either exhibits a reversal in the clade to LA (Fig. 166) or is synapomorphic only for DI, PY-SC, XI, BA, and WA (Fig. 167).

As mentioned above, the phylogenetic relationships of *Dilatris* and *Lachnanthes* are portrayed in two equally parsimonious topologies. In Figure 166 DI and LA are sister taxa, united by a single synapomorphy: the occurrence of bifurcate *and* trifurcate helicoid cyme units (character #6). Note that the presence of tapering trichomes with a basal rosette (character #13) is seen as an evolutionary event in the lineage preceding the DI-LA clade, and that a reversal of this feature (#13 R in Fig. 166) occurs along the clade to LA alone. The alternative and equally parsimonious possibility of independent evolution of such trichomes in the lineages to both DI and to WA, BA, XI, PY, & SC seems highly improbable. In Figure 167 the lineage terminating in *Dilatris* is depicted as arising after the lineage giving rise to *Lachnanthes*. Note that *Dilatris* is here united with WA, BA, XI, PY, and SC by character #13 (derivation of tapering trichomes with a basal rosette, requiring a single character state change and not two as in Fig. 166). In this scheme, changes in characters #6 (cyme bifurcate and trifurcate) and #33 (exine wall one-layered) may occur equally parsimoniously either as a pair of convergences (illustrated in Fig. 167) or as one unique event and a reversal (not illustrated).

Wachendorfia, *Barberetta*, *Xiphidium*, *Pyrrorhiza*, and *Schiekia* are members of the next monophyletic unit of the tribe. Three derived features support this grouping as seen in Figure 166: derivation of unicellular, tapering trichomes (character #10), a *reversal* to a superior ovary (char-

acter #39 R), and a reversal to an ovoid-globose seed shape (character #48 R*). *Pyrrorhiza* and *Schiekia* compose a monophyletic group by virtue of three synapomorphies. One of these, presence of a zygomorphic perianth (character #17 C), occurs independently in the lineage to *Wachendorfia*; however, this may be questionable, as will be discussed. The other two synapomorphies, anther dimorphism with one large and two caducous anthers (character #24) and a discontinuous inner subexterior exine layer (character #37), furnish excellent evidence for the close phylogenetic relationship of these taxa. *Wachendorfia* and *Barberetta* are a monophyletic assemblage as evidenced by five evolutionary steps (Fig. 166). Only two of these—presence of plicate leaves (character #3) and presence of large proximal verrucae on the pollen grains (character #32)—are nonhomoplasious, but these alone seem sufficient to warrant the monophyly of this group. *Xiphidium* is united with *Wachendorfia* and *Barberetta* by a single (rather weak) synapomorphy: occurrence of a simple cyme unit (character #5 R), a reversal from the occurrence of bifurcate cyme units, indicated as synapomorphic for the Haemodoraceae as a whole.

Character convergences and reversals. Certain characters exhibiting reversals or convergences in the cladogram of Figures 166 and 167 are worth discussing. The change in ovary position from superior to inferior (character #39) occurs before the initial bifurcation into two tribes. Thus, the inferior ovary found in DI, LA, HA, and all Conostylideae is interpreted as synapomorphic for the family as a whole (i.e., present in the common ancestor of the family but not in either immediate outgroup). A reversal of ovary position (character #39 R) occurs along the lineage to WA, BA, XI, PY, and SC. This is problematic in that the evolution of an inferior ovary is generally viewed as being irreversible and is often well correlated with other characters in general taxonomic studies. Such an assumption of irreversibility would require an additional three or four evolutionary steps in the most parsimonious cladograms of Figures 166 & 167. (See Alternative Cladograms and Figure 174 for consideration of the unique, irreversible evolution of an inferior ovary and of the independent evolution of an inferior ovary in two independent clades.)

Convergence in exine structural pattern is seen for *Lachnanthes* and *Haemodorum*. Even though both of these taxa have one-layered exine walls, the cladogram of Figure 166 supports the hypothesis that evolution of this exine wall type occurred independently in the lineages leading to the two taxa (character #33 C); as discussed above, the cladogram of Figure 167 permits an equally parsimonious alternative. The occurrence in *Haemodorum* of an occasional inner exine layer (see Simpson, 1983) may lend support to the lack of homology between *Lachnanthes* and *Haemodorum* in this feature and thus the convergent evolution of a one-layered exine.

Convergence in perianth symmetry (character #17 C) is seen in the lineages leading to WA and to PY-SC, arguing that a zygomorphic perianth evolved independently in these lineages. Similarly, the distinctive perianth apertures present in *Wachendorfia* and in *Schiekia* are portrayed as having been derived independently. But in view of the complexity of these perianth apertures, this possibility seems extremely unlikely. Because the monophyletic groupings of WA-BA and PY-SC are well supported by other characters (discussed above), it seems more likely that a reversal of perianth symmetry (zygomorphic to actinomorphic) occurred in the lineages to XI and to BA,

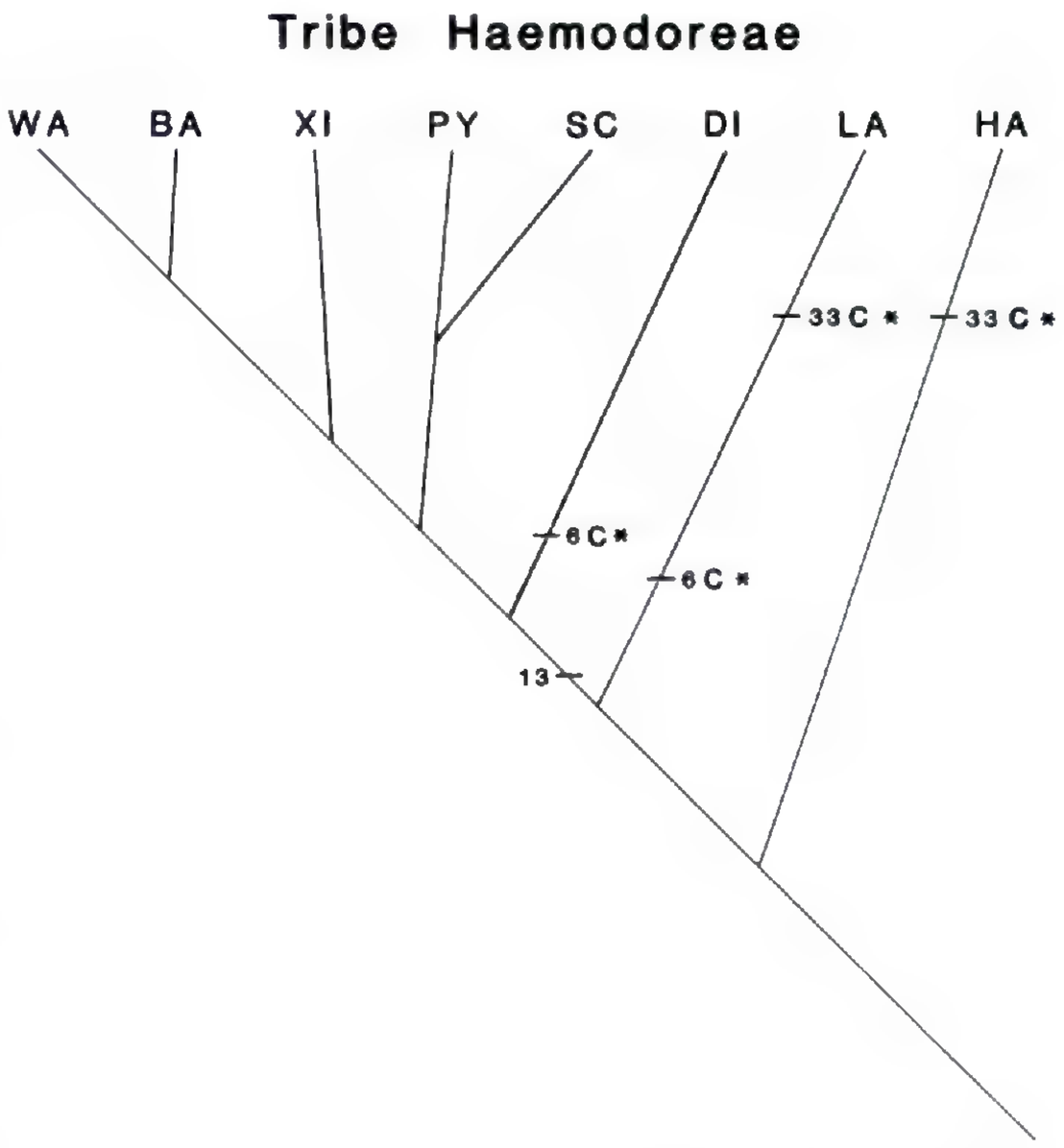


FIGURE 167. Second of two most parsimonious cladograms of the Haemodoraceae (only tribe Haemodoreae shown; tribe Conostylideae identical to that of Fig. 166). Only those character changes that differ from the cladogram of Figure 166 are listed. Character state changes indicated with a "*" (characters 6 and 33) have two equally parsimonious alternatives, either two convergent events or one apomorphy and one reversal; only the two convergent events (most likely in the author's view) are displayed in the cladogram. Abbreviations as in Figure 166.

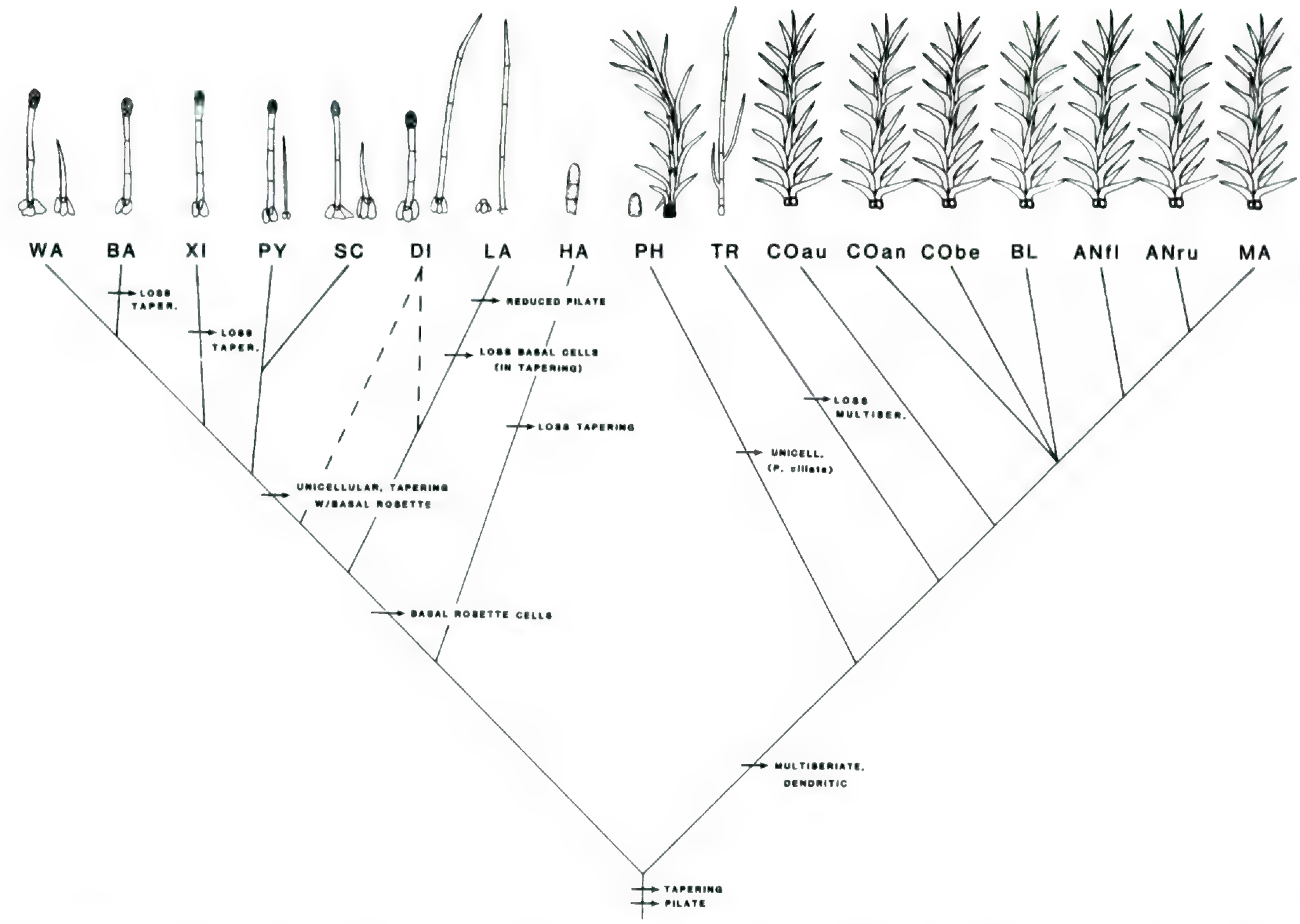


FIGURE 168. Superposition of illustrations of trichome anatomy on cladogram of Figures 166 and 167. Possible evolutionary changes in trichome anatomy are indicated.

and that a loss of perianth apertures occurred in the lineages to XI, BA, and PY. (See Alternative Cladograms, below, for a consideration of this possibility.)

A convergence in stamen number (character #22 C) occurs in the lineage to *Schiekia*. This convergence supports the idea that the staminodia in the outer whorl in *Schiekia* are not direct vestiges of ancestral stamens but rather are de novo floral modifications.

The loss of perianth tannin cells (character #20) occurs independently within each family tribe. The significance of this cell type is not known. Further anatomical studies or a chemical investigation of the precise contents of these tannin cells might be valuable.

Trichome evolution. The hypothesized homologies of trichome types in the Haemodoraceae can be assessed by a comparison of trichome anatomy with the branching patterns of the two most parsimonious cladograms (Fig. 168). First, it is most parsimonious to hypothesize that the common ancestor of the family (at the ingroup node) had pilate trichomes and uniseriate, tapering trichomes (which occur in members of both outgroup families). Second, the cladistic analysis supports the hypothesis of homology between the pilate trichomes of *Haemodorum* and those of the remaining Haemodoreae. The evolution of vestiture in *Haemodorum* involved the loss of ancestral tapering trichomes. Third, the distinctive trichome basal rosette evolved de novo in a separate lineage to that terminating in *Haemodorum*; the basal rosette cells may be correlated with further modification of the pilate trichome to one with a glandular terminal cell. The occurrence in *Lachnanthes* of long, uniseriate, tapering trichomes *lacking* a basal rosette is explained by the *loss* of that basal rosette; further evolutionary modifications in *Lachnanthes* involved the reduction of pilate trichomes to unicellular trichomes (having the basal rosette, however). The unicellular tapering trichomes (in PY, SC, and WA) evolved by reduction from a multicellular tapering trichome, and the presence of *only* pilate trichomes (in XI and BA) evolved by the independent loss of the unicellular type. In the tribe Conostylideae the most parsimonious explanation for the uniseriate, basally branched trichomes in *Tribonanthes* is reduction from the highly branched, dendritic type; the unicellular trichomes of *Phlebocarya ciliata* are portrayed as having arisen de

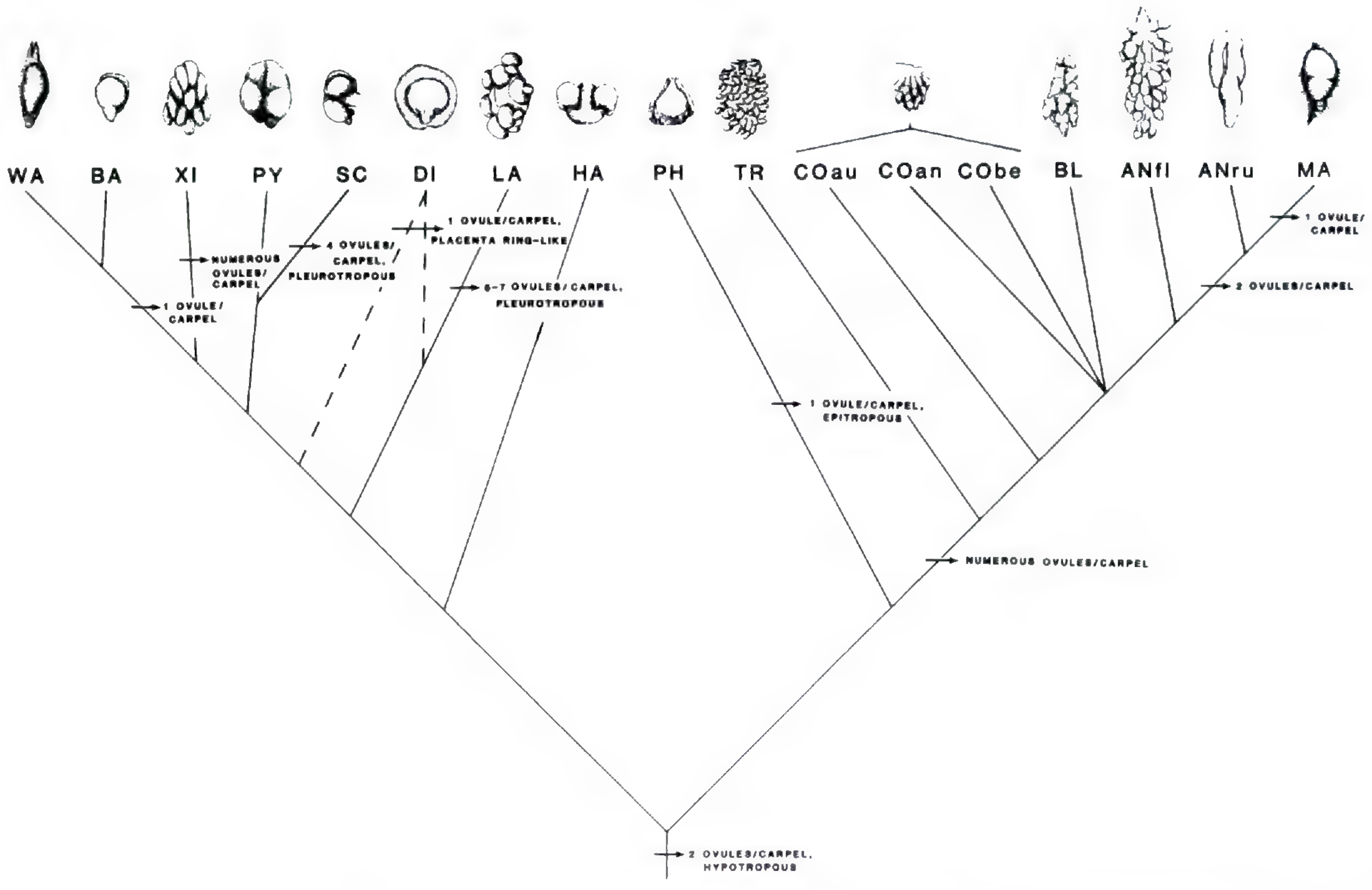


FIGURE 169. Superposition of illustrations of ovule morphology on cladogram of Figures 166 and 167. Possible evolutionary changes in ovule number, shape, and position are indicated.

novo (although it is possible they could be reductions from an ancestral pilate trichome).

Further studies of trichome anatomy in members of the Haemodoraceae may prove useful in confirming or refuting the above hypothesized homologies. Of particular value would be ultrastructural studies (e.g., details of cell wall structure or cytoplasmic contents) or developmental studies (e.g., cell division patterns in trichome ontogeny).

Ovule evolution. The evolution of ovule number and morphology in the Haemodoraceae is somewhat complicated, as seen in Figure 169. The most parsimonious explanation, following the morphocline of Figure 145, is that the ancestral condition for the family is two hypotropous ovules per carpel. An evolutionary step (to numerous ovules per carpel) occurs in the lineages to XI and to the TR-CO-BL-AN-MA clade. A reversal in ovule number from numerous to two per carpel occurs in the lineage to ANru. Reductions to one ovule/carpel occur independently in the clades to WA-BA, DI, PH, and MA. The epitropous ovule position in *Phlebocarya* occurs nowhere else in the family and is portrayed as an autapomorphy for the genus. The pleurotropous ovule position and increase in ovule number in *Lachnanthes* and *Schiekia* are most parsimoniously explained as being derived independently by convergence, which may seem doubtful in view of the distinctiveness of this morphology. The cladogram shows that a hypothesis of common ancestry for this feature in the two genera would necessitate two extra state changes. In fact, the rather thickened placental tissue of *Pyrrorhiza* and the ring of placental tissue in *Dilatris* may both be homologous with the thickened, peltiform placenta of, e.g., *Lachnanthes*. Developmental studies would be extremely informative in assessing the significance of placental morphology and of ovule number, shape, and position.

Seed evolution. As seen in Figure 170, the coded ancestral condition of seed morphology (elliptic, longitudinally ridged seeds) is not supported, as changes from this morphology are indicated in each tribal clade. A discoid, marginally winged seed morphology is portrayed as synapomorphic for the tribe Haemodoreae; presence of seed coat pubescence is synapomorphic for WA, BA, XI, PY, and SC (although this was not coded separately from the marginally winged condition in the analysis). A globose or globose-ovoid seed shape is portrayed as having evolved independently in the lineages to the SC-PY-XI-BA-WA clade and that of the Conostylideae. The flattened, marginally tomentose seeds of *Pyrrorhiza* are portrayed as having arisen de

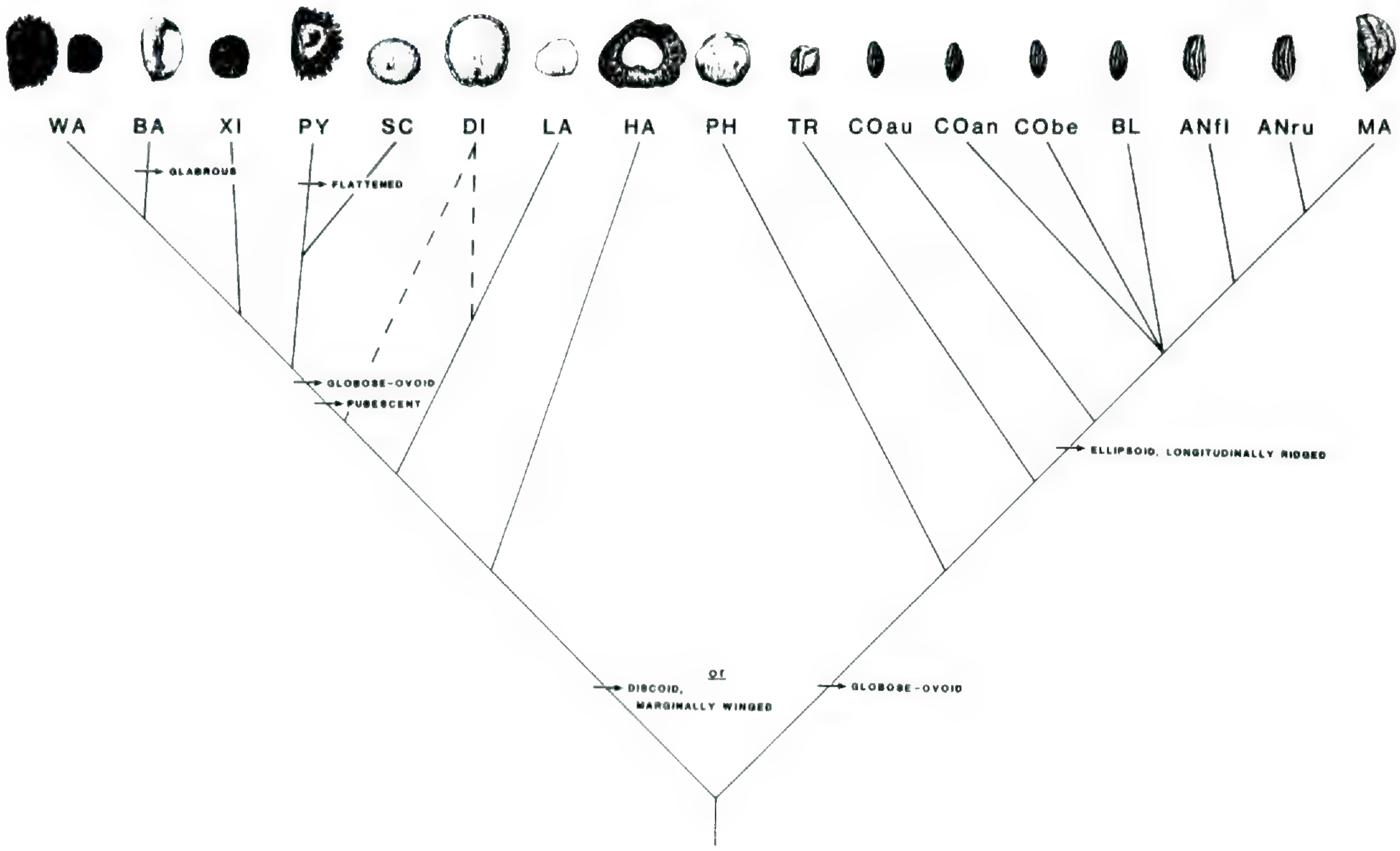


FIGURE 170. Superposition of illustrations of seed morphology on cladogram of Figures 166 and 167. Possible evolutionary changes in seed shape and vestiture are indicated. Note that other equally parsimonious evolutionary events may be possible.

novo, but an equally parsimonious explanation (not illustrated in Fig. 170) is that these flattened seeds are evolutionarily intermediate between the discoid, marginally winged seed and the globose-ovoid, pubescent seed type. In the tribe Conostylideae the ellipsoid, longitudinally ridged seed morphology is synapomorphic for CO, BL, AN, and MA. There is, therefore, no evidence that this seed type is plesiomorphic for either the family or the tribe Conostylideae, even though the seed morphology of both outgroups resemble it (see Character Analysis). It is the globose, glabrous seed type of *Phlebocarya* and *Tribonanthes* that is either synapomorphic for the tribe Conostylideae or possibly ancestral for the whole family. Future studies of seed anatomy and development may prove useful in assessing the homologies of seed evolution in the family.

Chromosome evolution. The cladogram of Figure 171 can be used to assess evolutionary changes in chromosome number in the Haemodoraceae. The two most basal taxa of each tribe have very similar chromosome numbers. Perhaps the most likely possibility is that the chromosome number for the common ancestor of the family was $n = 8$, which agrees with $n = 8$ as one of the more common chromosome counts among the outgroups; however, a base number of $n = 7$ is equally parsimonious. The common chromosome number of $n = 7$ for PH and TR is compatible with their close proximity on the cladogram (although not aiding in resolving their interrelationship) and can be explained possibly as an aneuploidy event from an ancestral $n = 8$ condition. Species of *Conostylis* have a variety of chromosome numbers, $n = 8$ being the most common. Figure 171 shows that the COan clade might be resolved from those of CObe and BL based on a common chromosome number ($n = 5$) with COau. However, the present study is much too incomplete to resolve interrelationships among *Conostylis* species; detailed studies of all species of this genus are needed to assess its karyological history better. A common chromosome number of $n = 6$ in AN and MA supports the very close relationship of these two genera.

Figure 171 portrays an evolutionary step from $n = 8$ to either $n = 15$ or $n = 24$ in the lineage that includes LA, DI, SC, PY, XI, BA, and WA. This event (a synapomorphy for this lineage in the cladistic analysis) could have arisen via tetraploidy or hexaploidy from an $n = 8$ ancestor. However, it is apparent that chromosome number evolution

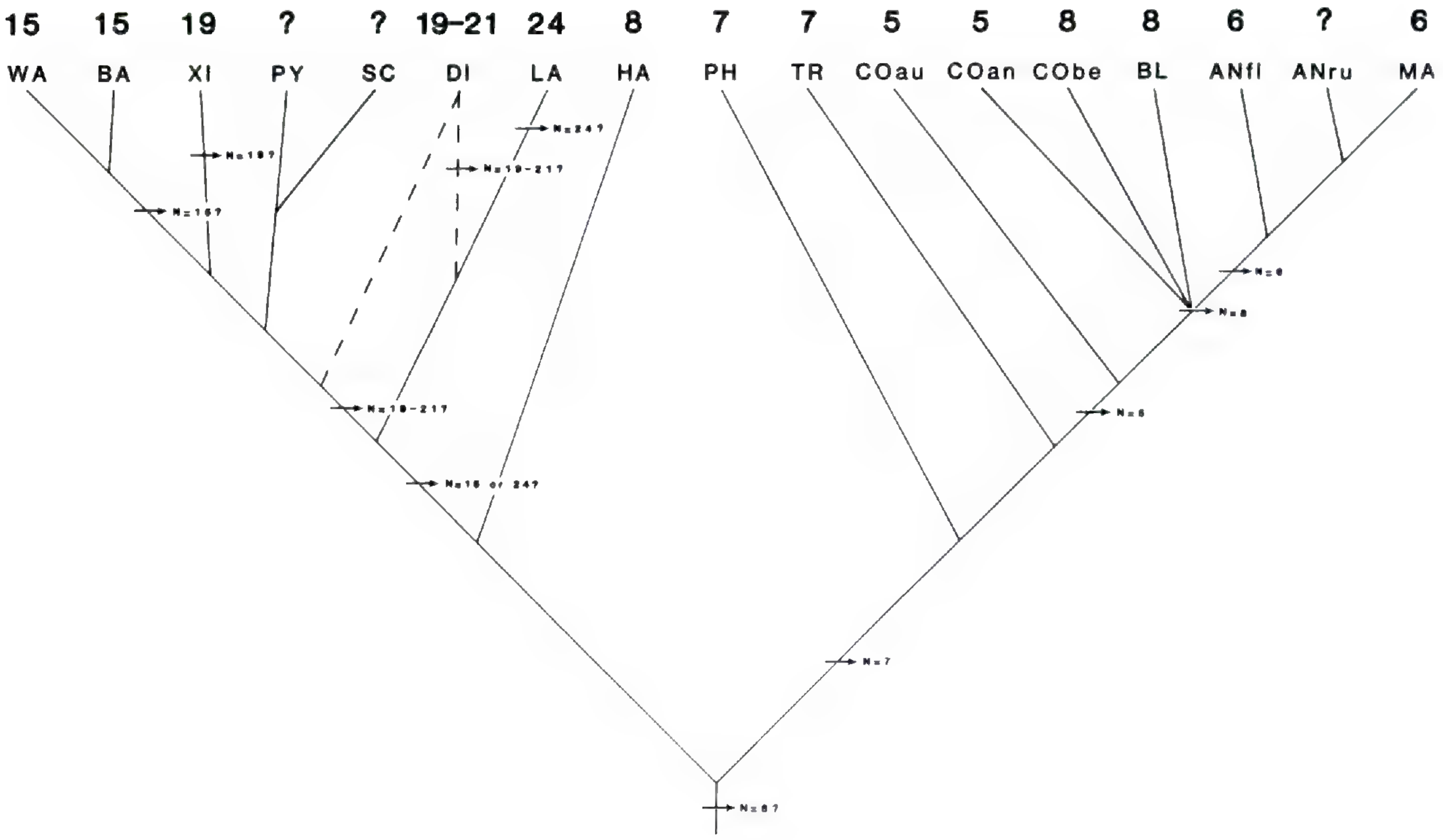


FIGURE 171. Superposition of haploid chromosome number on cladogram of Figures 166 and 167. Possible evolutionary changes in chromosome number are indicated. Note that other equally parsimonious evolutionary events may be possible.

in the tribe Haemodoreae is still virtually unresolved; numerous scenarios of evolutionary change are possible (Fig. 171). Although chromosome number is a valuable taxonomic character, there are problems due to ambiguity of character coding (see Character Analysis) and lack of data. Future karyotypic studies and determination of chromosome numbers for *Pyrrorhiza* and *Schiekia* should aid greatly in testing the hypotheses of Figure 171 and in refining phylogenetic relationships, particularly in the tribe Haemodoreae.

Biogeography. The cladograms of Figures 166 & 167 can be used to assess the biogeographic history of the Haemodoraceae. It should be stressed that biogeographic data, being extrinsic data, were not included in the original data set. As seen in Figure 172, all members of the tribe Conostylideae are restricted to southwestern Australia. *Haemodorum*, the most basal genus of the tribe Haemodoreae, is the only other Australasian member of the family, being distributed in western, northern, and eastern Australia, Tasmania, and parts of New Guinea. This distributional pattern can be explained most simply by a single vicariance event: the splitting of a continuous ancestral population via the separation of (or establishment of an effective reproductive barrier between) Australia–Antarctica from the remainder of Gondwanaland. That portion remaining on Australia–Antarctica eventually gave rise to *Haemodorum*; the ancestral stock remaining on South America–Africa eventually diverged to give rise to the seven other genera of the tribe (Fig. 172). The present distributions of *Pyrrorhiza*, *Schiekia*, *Xiphidium*, *Wachendorfia*, and *Barberetta* could be explained by a single vicariance event: the continental separation of South America and Africa at the point of divergence of the lineages to XI and to WA-BA. As is evident from Figure 172, the phylogenetic relationship of *Dilatris* is problematic with respect to vicariance biogeography. If *Dilatris* is accepted as the sister taxon of *Lachnanthes* (as in Fig. 166), then it could be hypothesized that the splitting of the lineages to *Dilatris* and *Lachnanthes* was via vicariance: the separation of an ancestral population (with subsequent divergence) by the splitting of South America from Africa. *Lachnanthes* could then have attained its present distribution via dispersal or vicariance from South America to North America. This possibility would necessitate an independent (but contemporaneous) vicariance event at the point of divergence of the lineages to XI and to WA-BA. If *Dilatris* is accepted as being the sister taxon to WA, BA, XI, PY, and SC (as in Fig. 167), then its present distribution is most simply explained as long-distance dispersal (Fig. 172). The fact that *Dilatris* and *Wachendorfia* are sympatric over much of their range may be evidence that they attained a common range by

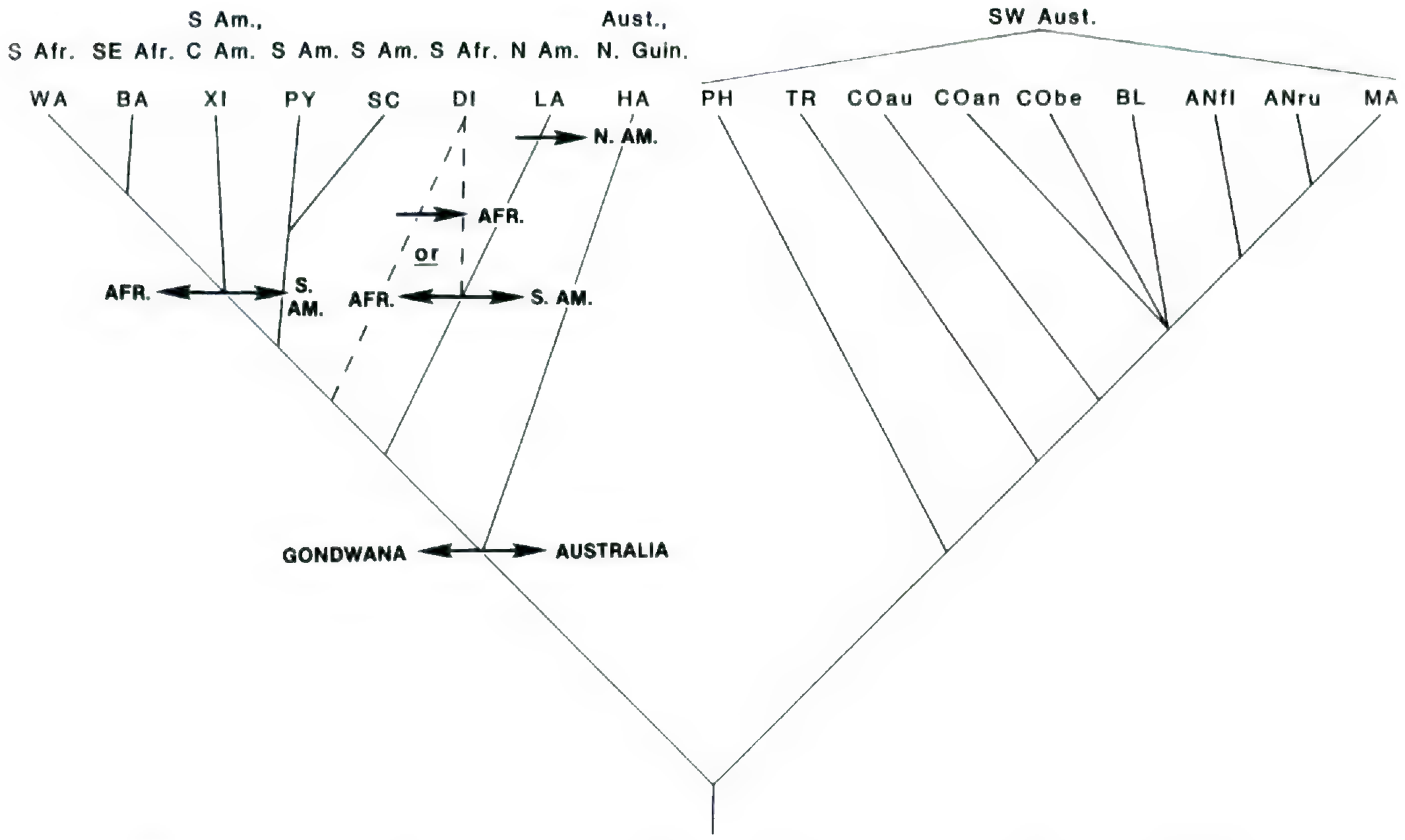


FIGURE 172. Superposition of geographic ranges on cladogram of Figures 166 and 167. Arrows represent major biogeographic changes, including possible vicariance events (double arrows) and dispersals (single arrows).

separate biogeographic processes (Croizat et al., 1974).

Alternative cladograms. In view of the incompatibility of certain character changes in the cladograms of Figures 166 & 167, a few alternative cladistic relationships are worth consideration. One major possibility is that an inferior ovary evolved uniquely and irreversibly in the Haemodoraceae; the resultant cladogram is seen in Figure 173. This topology requires 92 total character state changes (C.I. = 0.598), a length of four state changes greater than the most parsimonious solution of Figures 166 & 167. Note that in Figure 173 the traditionally defined tribe Haemodoreae is now paraphyletic, with *Dilatris*, *Haemodorum*, and *Lachnanthes* more closely related to the six genera of the Conostylideae (the sole synapomorphy being an inferior ovary, character #39) than to other traditionally classified Haemodoreae. This alternative cladogram contains additional problems of conflicting character state changes. These include introduced homoplasy in presence/absence of pilate trichomes with basal rosette cells (character #8), placental sclereids (character #43), seed vestiture (character #50), and chromosome number (character #51). It seems particularly unlikely, for example, that there would have been a secondary decrease in chromosome number (to $n = 8$ in the lineage to *Haemodorum*) as well as the loss (for the Haemodoraceae as a whole) and reacquisition (in the lineage to the Conostylideae) of placental sclereid cells. However, in view of the generally accepted irreversibility of ovary position, the cladogram of Figure 173 is a possible alternative to the more parsimonious cladograms of Figures 166 & 167. Detailed investigation of ovary development and floral vasculature might prove extremely valuable in assessing the uniqueness and irreversibility of the evolution of ovary position in the Haemodoraceae.

Another alternative portrays the independent evolution of an inferior ovary in the Conostylideae and in one clade of the Haemodoreae (Fig. 174A; length = 90; C.I. = 0.611). Such a topology would link DI, LA, and HA as members of a monophyletic group (as in Fig. 173) within the tribe Haemodoreae; synapomorphies for these three genera are: exine one-layered (character #33, necessitating a reversal in lineage to DI, although two convergent events is equally parsimonious), inferior ovary (character #39, convergent in lineage to all members of tribe Conostylideae, although a unique event plus a reversal is equally parsimonious), and discoid seed shape (character #48). Of these, the convergent evolution of an inferior ovary and discoid seeds seem most likely to be synapomorphies for the three genera. The cladogram of Figure 174A is, of course, less parsimonious (two steps greater) than that of Figure 166 or 167 and necessitates

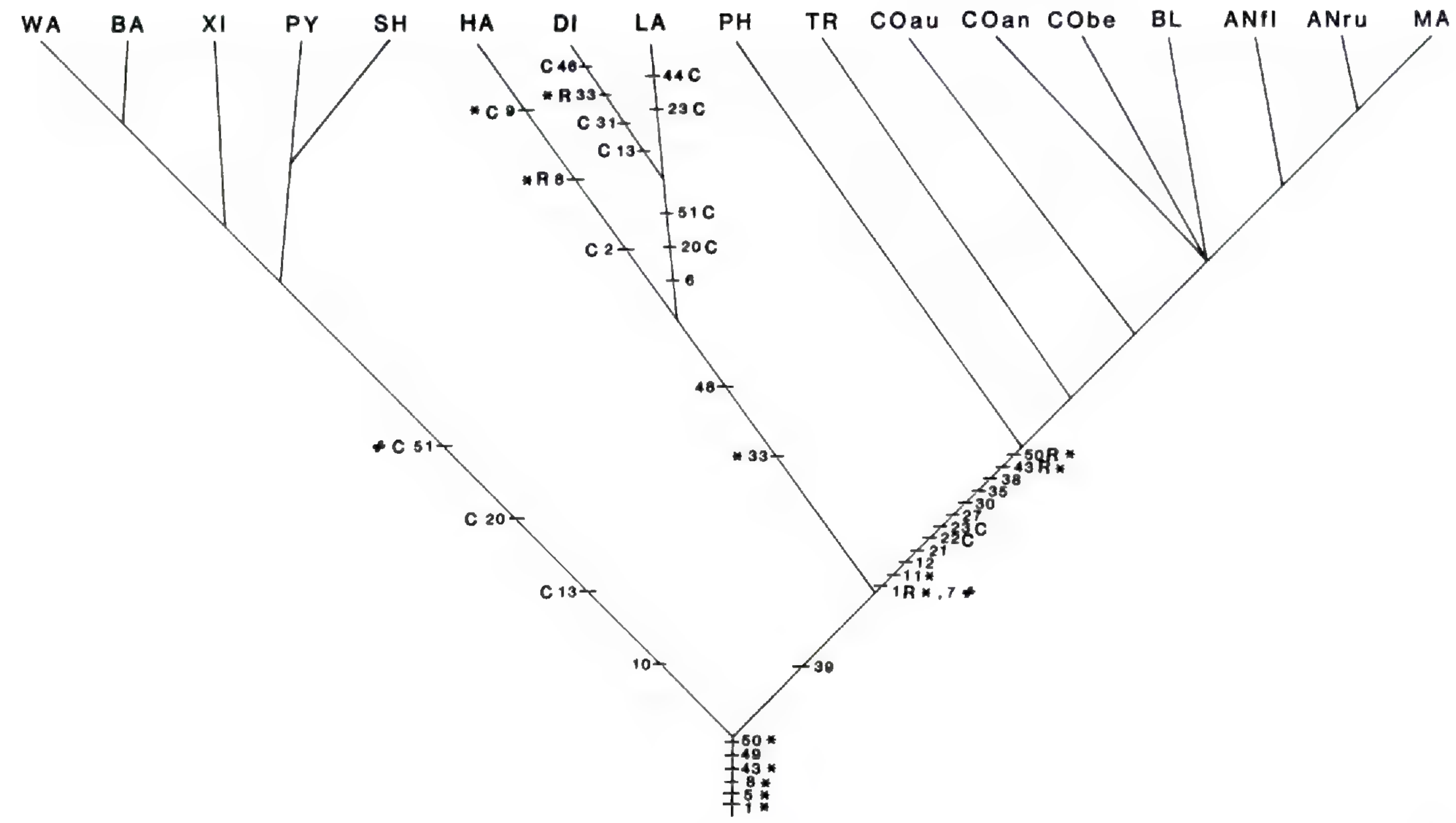


FIGURE 173. Alternative cladogram (to Figs. 166, 167): most parsimonious cladogram in which an inferior ovary position evolves uniquely and irreversibly. Only those characters below the divergence of PY-SC and of PH are listed; all other state changes are identical to Figures 166 and 167. Character state changes indicated with a "*" have two equally parsimonious alternatives, either two convergent events or one apomorphy and one reversal; only one of these alternatives (the most likely in the author's view) is displayed in the cladogram.

additional homoplasy for some characters, including: trichome anatomy (characters #8 R and #13 C), perianth tannin cells (character #20 C, an additional convergence portrayed), and chromosome number (character #51C).

A third alternative cladogram is presented in Fig. 174B. This possibility differs from the most parsimonious topology of Figures 166 & 167 in placing the lineage to XI basal to that of PY-SC (i.e., in portraying WA-BA and PY-SC as sister groups). Figure 174B requires only a single extra step (length = 89; C.I. = 0.618) compared with the cladograms of Figures 166 & 167. In fact, the phylogenetic relationship of *Xiphidium* as portrayed by Figures 166 & 167 could be viewed as questionable. This most parsimonious explanation, that *Xiphidium* is most closely related to the WA-BA subgroup, is supported by only one synapomorphy: presence of simple cyme units (character #5). The rationale for perhaps preferring the cladogram of Figure 174B is that it is more parsimonious than the cladogram of Figures 166 & 167 *if* it is assumed that zygomorphic perianth symmetry (character #17) and perianth apertures (character #13) are homologous when present (i.e., that they arose by common evolutionary origin, not by convergence). If, for example, the common possession of a zygomorphic perianth is synapomorphic for WA, PY, and SC (as seen in Fig. 174B), then one fewer reversal for this character occurs in the cladogram of Figure 174B (vs. those of Figures 166 & 167). In addition, if perianth apertures arose in WA and SC by a single evolutionary event (at "+" sign in Fig. 174B), then one fewer reversal (i.e., loss of perianth apertures) is required in Figure 174B than is required in Figures 166, 167. It is the author's view that each of these are very likely possibilities, particularly with regard to the distinctive perianth apertures of *Wachendorfia* and *Schiekia*. Thus, the cladogram of Figure 174B is to be preferred over that of Figures 166 & 167 (at least with respect to these five genera of the Haemodoreae) even though it is overall less parsimonious by one step. This reasoning is, in effect, a type of a posteriori weighting of characters. It is similar to utilizing "Dollo" character parsimony, which allows no convergences and minimizes any subsequent character state reversals.

A fourth possible alternative cladogram (length = 90; C.I. = 0.611) is that of Figure 175A, which portrays DI as the sister group of WA-BA, the three taxa united by two synapomorphies: a pollen apertural border (character #31) and a single ovule/carpel (character #46 C). However, this topology is difficult to explain in view of a host of

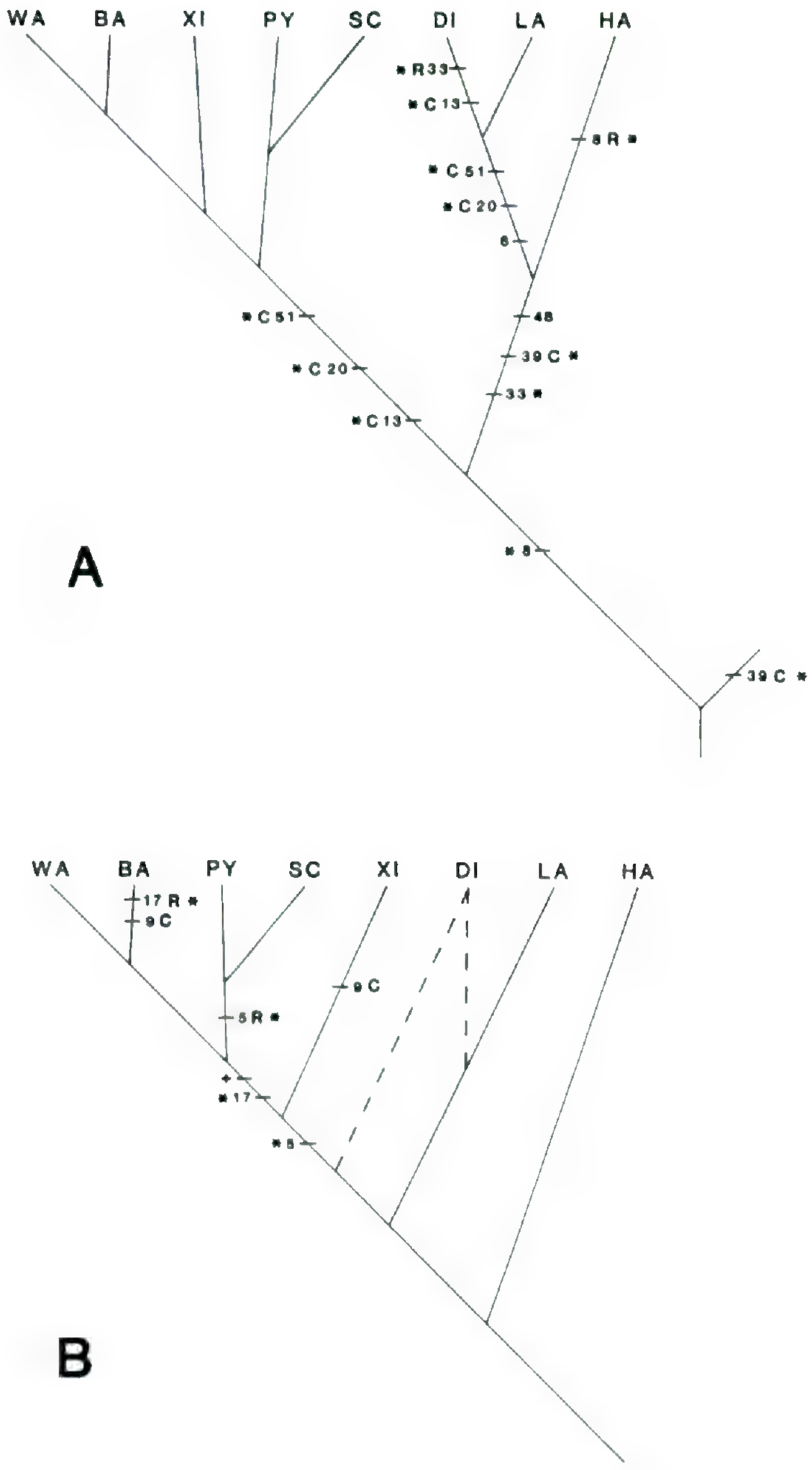


FIGURE 174. Alternative cladograms (to Figs. 166, 167). Only those characters that differ in distribution from Figure 166 are listed. Character state changes indicated with a "*" have two equally parsimonious alternatives, either two convergent events or one apomorphy and one reversal; only one of these alternatives (the most likely in the author's view) is displayed in the cladogram.—A. Alternative cladogram (only tribe Haemodoreae shown) portraying *Dilatris*, *Lachnanthes*, and *Haemodorum* as members of a monophyletic assemblage.—B. Alternative cladogram (only tribe Haemodoreae shown) portraying *Wachendofia–Barberetta* and *Pyrrorhiza–Schiekia* as sister groups.

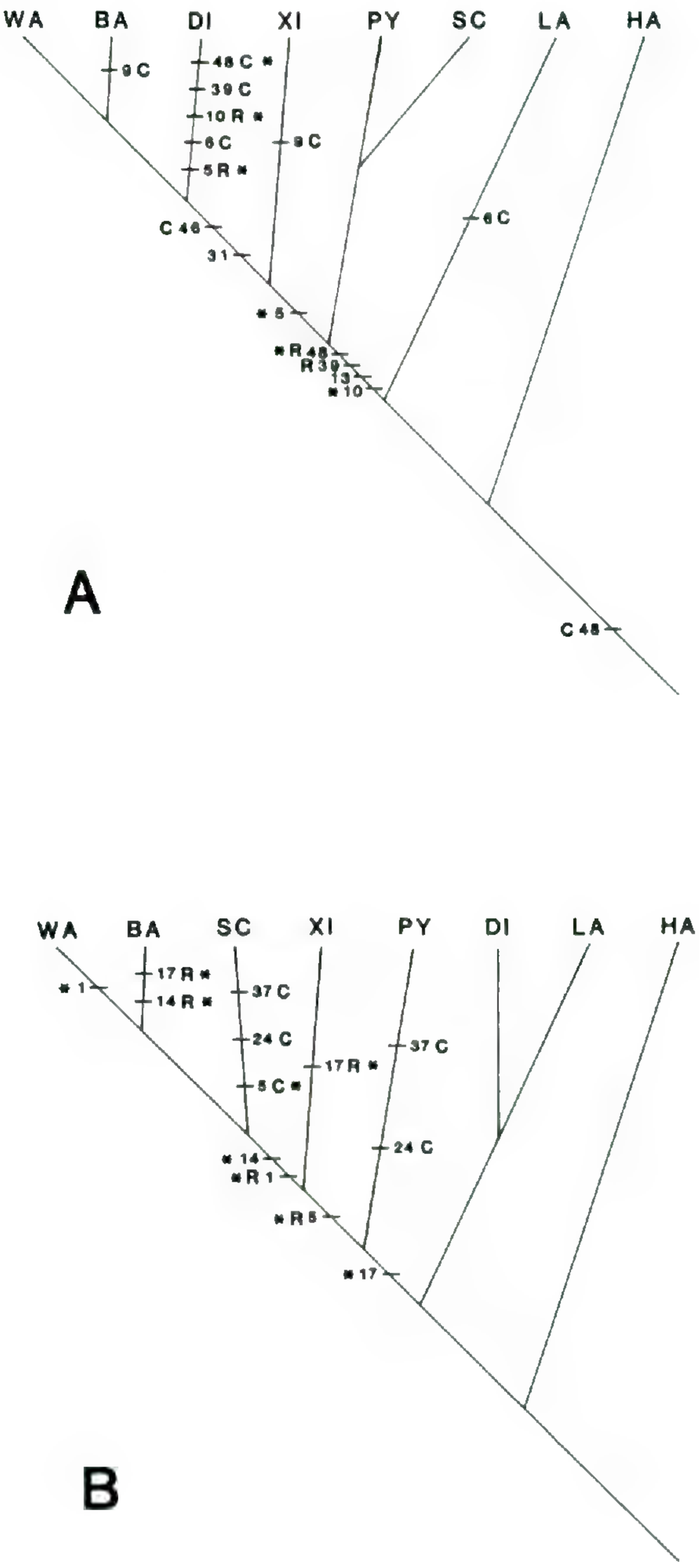


FIGURE 175. Alternative cladograms (to Figs. 166, 167). Only those characters that differ in distribution from Figure 166 are listed. Character state changes indicated with a "*" have two equally parsimonious alternatives, either two convergent events or one apomorphy and one reversal; only one of these alternatives (the most likely in the author's view) is displayed in the cladogram.—A. Alternative cladogram (only tribe Haemodoreae shown) portraying *Dilatris* as the sister group to *Wachendorfia–Barberetta*.—B. Most parsimonious cladogram (only tribe Haemodoreae shown) portraying *Schiekia* as the sister group of *Wachendorfia–Barberetta*.

other characters and necessitates additional homoplasy in, e.g., inflorescence type (characters #5, #6), trichome anatomy (character #10), ovary position (character #39), and seed shape (character #48 C). Homoplasy in ovary position, trichome anatomy, and seed morphology is particularly difficult to reconcile in view of similarities of *Dilatris* with LA and HA. Thus, the cladogram of Fig. 175A cannot, in the author's opinion, be readily supported over that of Figures 166 and 167.

A final alternative cladogram (length = 92; C.I. = 0.598) is portrayed in Figure 175B. This alternative differs from that of Figures 166 & 167 in removing *Schiekia* as the sister group of *Pyrrorhiza* and placing it as the sister group of WA-BA. Figure 175B has the advantage of treating the distinctive perianth apertures of *Wachendorfia* and *Schiekia* as nonparallel features, necessitating a loss only in the clade to *Barberetta*. However, the evidence for uniting *Schiekia* and *Pyrrorhiza*,

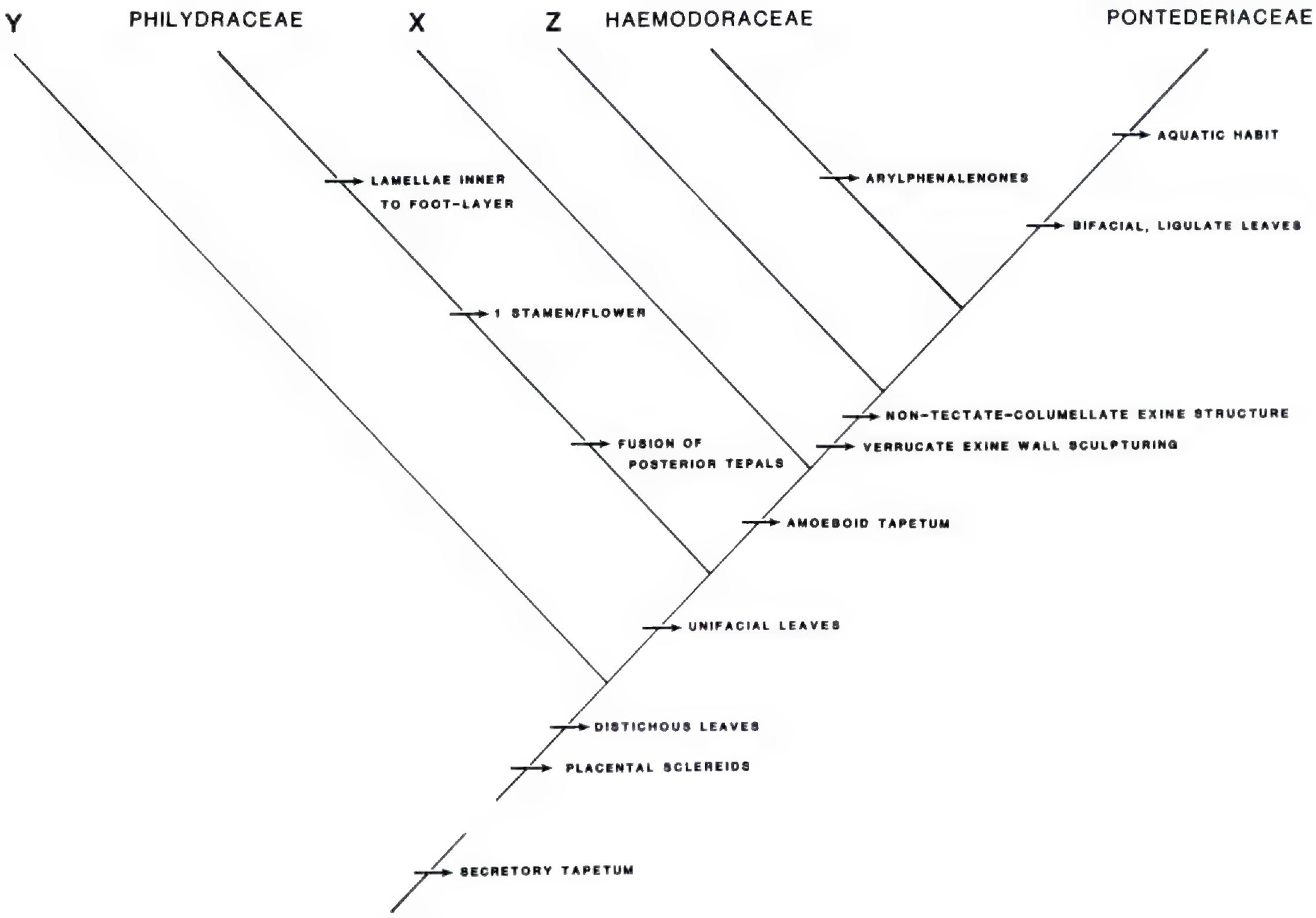


FIGURE 176. Cladogram portraying hypothesized relationships among the Haemodoraceae, Pontederiaceae, and Philydraceae. Major evolutionary events are portrayed. Note possible clades to "X," "Y," and "Z." (See text for discussion.)

based on exine ultrastructure (character #37) and on stamen/staminode morphology (character #24) seems, to the author, more convincing. The cladogram of Figure 174B is accepted as more likely than that of Figure 175B.

Of the above alternative, but less parsimonious, cladograms, that of Figure 175A is most compatible with a vicariance explanation of present distributional ranges. This cladogram would require only two separate vicariance events correlated with the splitting of Gondwanaland into Australia, Africa, and South America. The distribution of *Lachnanthes* could, as above, be explained via dispersal or a vicariance event between South and North America. However, as discussed, acceptance of this cladogram would necessitate several unlikely homoplasious events. Thus, it must be concluded that, despite the better biogeographic "fit" of the alternative cladogram of Figure 175A, the data support those of Figures 166 & 167 (or, perhaps, of Figure 174B) better.

Interfamilial relationships. Although a strict cladistic analysis of the Haemodoraceae and all possible outgroup families in the complex is beyond the scope of this paper, a major premise of the present analysis is that the families most closely related to the Haemodoraceae are the Philydraceae and Pontederiaceae (see Outgroup Taxa). The cladogram of Figure 176 illustrates major hypothesized evolutionary changes among lineages leading to the Philydraceae, Pontederiaceae, and Haemodoraceae, including those treated as characters (#53–55) in the cladistic analysis of the Haemodoraceae. One or more autapomorphies are shown for each terminal clade, evidence that the three families are monophyletic. The cladogram was rooted at the Philydraceae under the assumption that the unique exine structure of the Haemodoraceae and Pontederiaceae (found in no other considered outgroup family) constitutes a very reliable synapomorphy and unites the latter two families as sister taxa. In addition to the evolution of unifacial leaves (character #55 in the cladistic analysis), a possible synapomorphy linking the three families is the presence of placental sclereids and perianth tannin cells. An amoeboid tapetum (character #53) and a non-tectate-columellate, verrucate exinous pollen wall (character #54) constitute synapomorphies for the Haemodoraceae and Pontederiaceae. It is hypothesized that evolution of the Pontederiaceae involved a major adaptive shift and

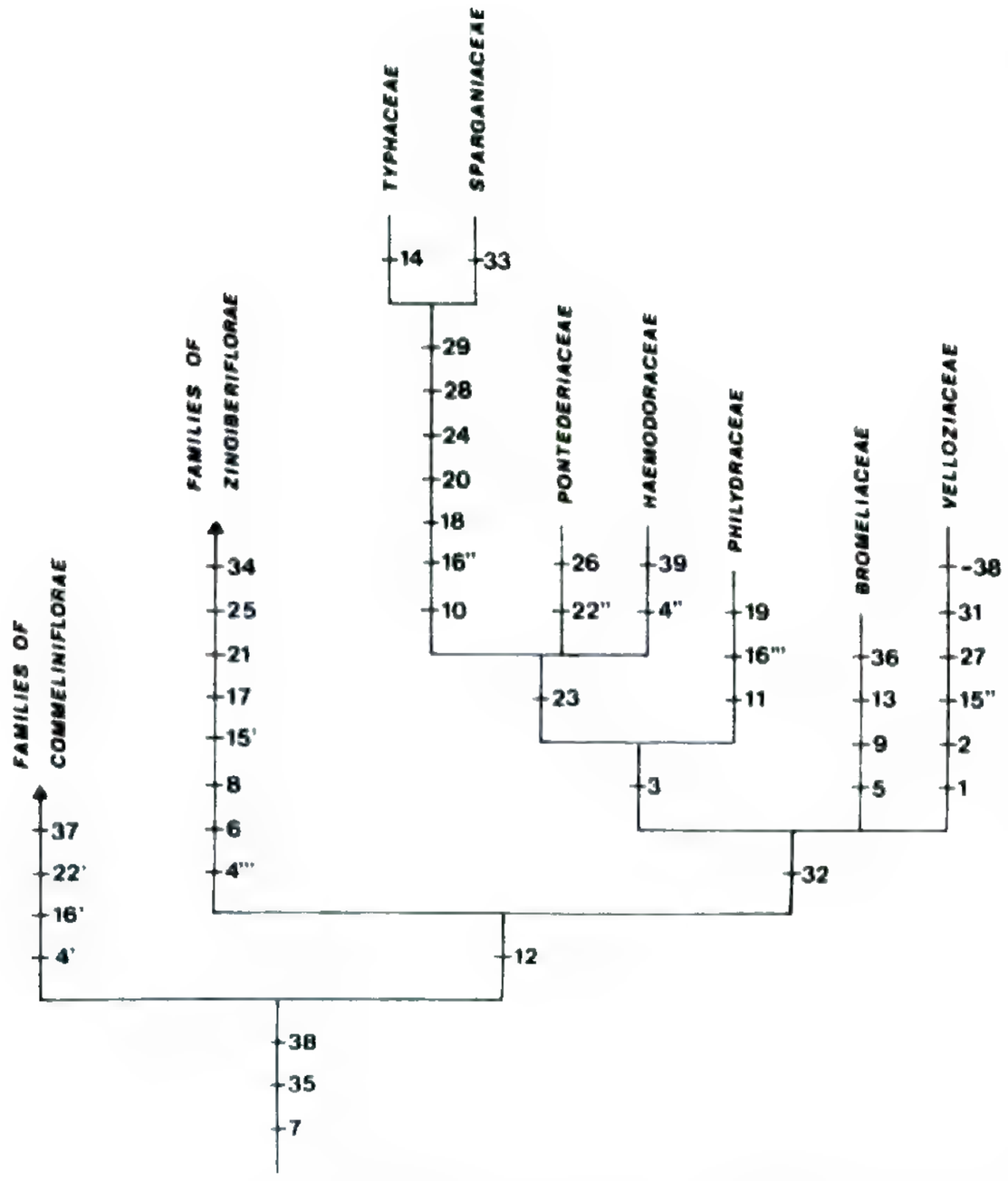


FIGURE 177. Cladogram of the Bromeliiflorae, reprinted from Dahlgren & Rasmussen (1983).

radiation to an aquatic environment with subsequent changes in anatomy, such as the development of spongy aerenchyma in some taxa. This shift to a free-floating or emergent growth form may be correlated with an evolutionary change from unifacial to bifacial leaf morphology. This hypothesis is supported by the fact that the Pontederiaceae typically have inverted vascular bundles analogous to a "radial" (unifacial) origin (Arber, 1925, and references therein).

The grouping of the Philydraceae, Pontederiaceae, and Haemodoraceae as a monophyletic group (Fig. 176) agrees well with the delimitation of the Pontederiinae, sensu Walker (1986). Figure 176 shows many similarities as well with the eclectic cladistic portrayal of the Bromeliiflorae, sensu Dahlgren & Rasmussen (1983; see Fig. 177). Dahlgren & Rasmussen portrayed the Typhales (Sparganiaceae and Typhaceae) in a tritomy with the Haemodoraceae and Pontederiaceae; the Philydraceae are basal to this clade (Fig. 177). I propose the existence of synapomorphies, derived primarily from palynological data, linking the Haemodoraceae and Pontederiaceae as sister taxa. Dahlgren & Rasmussen linked the Typhales to the Pontederiaceae and Haemodoraceae via a single synapomorphy: presence of an amoeboid tapetum. Because investigated members of *Typha* and *Sparganium* have a typical tectate-columellate architecture, it is possible that the lineage to the Typhales could be placed in Figure 176 at "X," i.e., before the evolution of the palynological specializations. In addition, at least one species of the Typhales, *Sparganium eurycarpum*, possesses placental sclereids similar to those found in the Haemodoraceae, Philydraceae, and Pontederiaceae. However, in view of the lack of additional supporting evidence, the linkage of the Typhales to the Haemodoraceae–Pontederiaceae seems quite speculative. Based on these few characters, it is equally parsimonious to hypothesize the cladistic position of the Typhales at "Y" in Figure 176 (assuming the Typhales to belong within the Bromeliiflorae to begin with). This possibility requires the independent origin of an amoeboid tapetum but no reversal to a bifacial leaf. It is apparent that the numerous specializations possessed by the Typhales have obscured their affinities. The relationship of the Typhales to other monocotyledons continues to be an intriguing systematic problem (see Dahlgren & Clifford, 1982).

In contrast to Dahlgren & Rasmussen (1983), Walker (1986) placed the Zingiberiflorae (Zingiberales) as the sister taxon of his Pontederiiflorae (= Pontederiidae; including the Haemodoraceae, Philydraceae, and Pontederiaceae), equivalent to position "Y" in Figure 176. This would fit the distribution of characters in Figure 176 fairly well, as the Zingiberales have mostly distichous leaves (possibly an ancestral character) and at least one species, *Strelitzia reginae*, has placental sclereids similar to those in the Haemodoraceae, Philydraceae, and Pontederiaceae (Simpson, unpublished). However, the Zingiberales possess an amoeboid (not secretory) tapetum, requiring either an independent evolutionary event in the Zingiberales or the separate evolution of a secretory tapetum in the lineage to the Philydraceae. One other possibility is worthy of consideration: that the Zingiberales are the sister group of the Haemodoraceae–Pontederiaceae (position "Z" in Fig. 176). This cladistic hypothesis would necessitate the independent evolution of a bifacial leaf morphology. However, it is intriguing that all members of the Zingiberales have a thin, modified exine wall, often consisting of scattered deposits atop a thick, cellulosic/pectic intine (Kress et al., 1978). In addition, ultrastructural developmental studies by the author (Simpson, 1989) indicate that early exine deposition in *Xiphidium* (Haemodoraceae) is strikingly similar to that occurring in *Heliconia* of the Zingiberales (see Stone et al., 1979). In both taxa sporopollenin is deposited on one to several extruded "white lines," defining an inner and outer exine layer. Thus, the two-layered nature of the exine in most Haemodoraceae may be structurally

homologous with that found in at least one member of the Zingiberiflorae. This developmental evidence would argue for the placement of the Zingiberales at "Z" in Figure 176. Further studies of pollen wall development, especially in other families of the Bromeliiflorae, sensu Dahlgren & Rasmussen (1983) may prove extremely useful in confirming the distinctiveness of this developmental pattern in these taxa.

Conclusions

It is hoped that the detailed description of the characteristics of the Haemodoraceae and of the rationale for character coding will serve as a basis for future criticism and refinement of the phylogenetic relationships presented. The occurrence of incompatibilities between several characters makes difficult any reasonable certainty of phylogenetic relationships among some genera. The interrelationships among the tribe Haemodoreae pose a particular problem. Aside from certain groupings (such as the sister-group relationships of *Pyrrorhiza* and *Schiekia* and of *Wachendorfia* and *Barberetta*), several other possibilities having a minimum of additional evolutionary steps are evident. Recent analyses using alternative coding schemes (emphasizing unordered coding) and new data obtained since this paper went to press have yielded three additional most parsimonious trees for the tribe Haemodoreae; each of these topologies inincludes *Dilatris*, *Haemodorum*, and *Lachnanthes* as a monophyletic clade most closely related to *Pyrrorhiza–Schiekia*. These possibilities will be considered in light of future research (see below). The major phylogenetic relationships of the Conostylideae appear at this time to be rather firm, with the possible exception of the interrelationships of *Phlebocarya* and *Tribonanthes*. As was emphasized, critical analysis of many more species of *Conostylis* and *Anigozanthos* is needed before their interrelationships can be understood. The included studies suggest, however, that *Conostylis* and *Anigozanthos*, as usually circumscribed, are very likely not monophyletic groups. Merging of *Blancoa* with *Conostylis* and *Macropidia* with *Anigozanthos* may be warranted in a strict phylogenetic classification.

Consideration of the Haemodoraceae and immediate allies are pivotal in analyzing the validity of the Bromeliiflorae sensu Dahlgren & Rasmussen. In fact, a major discordance in the classification of monocots proposed by Walker (1986) versus that of Dahlgren and coworkers centers on the recognition of the Bromeliiflorae and their relationships to the Zingiberales and Commelinidae. Future investigations of the interfamilial relationships of the Haemodoraceae should prove quite intriguing in this regard.

The present study underscores the need for additional research, particularly in karyology, ultrastructure, and development. My current project on morphometric analysis of ovule and seed development in the complex might prove particularly intriguing in tracing discrete evolutionary events. A better understanding of biogeographic history and ecology could provide insight into the possible adaptive significance of these events. Finally, the relatively new techniques of DNA restriction site analysis and sequencing could provide very important data in validating or refuting proposed relationships. This study serves well to exemplify that the problems and uncertainties typically evident in phylogenetic analyses may lead to future research that will further clarify relationships and present new insights into plant evolution.

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A CONTRIBUTION TO THE STUDY OF POLLEN WALL ULTRASTRUCTURE OF ORCHID POLLINIA[1]

Michael S. Zavada[2]

ABSTRACT

Pollen grains of 30 orchid species from the Spiranthoideae and Epidendroideae (including the Vandeae) were studied ultrastructurally. This study complements the published palynological literature on the Apostasioideae, Cypripedioideae, Spiranthoideae, and Orchidoideae. The orchid pollen thus far studied exhibits a wide range of variation in pollen unit, aperture type, and wall ultrastructure. The least specialized Apostasioideae and some Cypripedioideae shed pollen in monads and have monosulcate grains with a tectate-columellate, perforate exine structure. These are features observed in most primitive monocotyledons. In the more specialized orchid subfamilies, pollen occurs in mealy or tightly packed, waxy pollinia, and the grains have a porate-ulcerate aperture or are inaperturate, and the sporopolleninous wall is present only on the most peripheral grains in the pollinium (a few species lack exines). The presence of the exine on only the most peripheral grains in the pollinium is accompanied by a loss of the footlayer in many taxa and elaboration of the intine. As in other monocots, endexine has not been unequivocally demonstrated in orchids.

The Orchidaceae comprise about 1,000 genera and 15,000–20,000 species. Dressler (1981, 1983) has separated the orchids into five subfamilies: Apostasioideae, Cypripedioideae, Spiranthoideae, Orchidoideae, and Epidendroideae (including the Vandeae).

There is general agreement among taxonomists that the Apostasioideae are the least specialized (primitive) subfamily of the Orchidaceae (Dressler & Dodson, 1960; Dressler, 1981, 1983), with two genera and about 16 species, found primarily in tropical Asia. Pollen morphology and ultrastructure have been investigated (Schill, 1978; Newton & Williams, 1978) and the pollen shows features of many other monocots (Zavada, 1983). The grains of the Apostasioideae are usually shed in monads and are monosulcate. Exine sculpturing is reticulate. Pollen wall structure is tectate-columellate with a thin footlayer and no endexine.

The Cypripedioideae, primarily a tropical group, have four genera and about 130 species. This subfamily likewise exhibits many primitive features (Ackerman & Williams, 1980, 1981). Pollen is generally monosulcate or ulcerate (i.e., with an ill-defined pore). Exine sculpturing can be reticulate or verrucate to scabrate. The pollen wall infrastructure, as revealed by SEM, appears to be columellate (Newton & Williams, 1978; Schill & Pfeiffer, 1977).

Representative taxa of the rather large subfamily Spiranthoideae have been investigated palynologically to some extent (Balogh, 1979; Williams & Broome, 1976). Pollen grains are shed in loose pollinia and are generally inaperturate. Exine sculpturing is reticulate (especially in the Spiranthinae), and wall structure varies depending on the position of the pollen grain in the pollinium: peripheral grains are usually tectate-columellate with a thick footlayer; those in the interior of the pollinium usually lack the tectum, with only the columellae and footlayer being present.

Pollen of the Spiranthoideae and Epidendroideae have been little studied using transmission electron microscopy (however, see examples in Chardard, 1958, 1969; Heslop-Harrison, 1968; Dulieu 1973; Caspers & Caspers, 1976; Balogh, 1982; Balogh & Mann, 1982; Hesse & Burns-Balogh, 1984; Wolter & Schill, 1986). The present contribution describes the pollen wall structure of 30 taxa from these subfamilies (only one taxon from the Spiranthoideae).

METHODS

Pollinia were removed from living material and placed immediately in cacodylate HCl-buffered glutaraldehyde-formaldehyde, followed by fixation in osmium tetroxide, dehydration in an ethanol series, and embedding in Dow Epoxy Resin 334. Pollinia were sectioned on an LKB–1 ultramicrotome, se-

[1] I thank Tim Reeves and Eric Christenson for providing the live material used in this study.
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quentially poststained in uranyl acetate and lead citrate for 15 minutes, and viewed with a Philips EM-300 transmission electron microscope. Vouchers for all live specimens have been deposited in the herbaria CONN or MRD (Appendix 1). The classification used follows Dressler (1981, 1983).

Descriptive Palynology

SPIRANTHOIDEAE
Erythrodeae–Spiranthinae

Sacoila lanceolata (Aubl.) Garay. Pollen grains occur in loosely packed pollinia and are inaperturate. Exine sculpturing is reticulate and pollen wall structure varies depending on the position of the pollen grain in the pollinium. Pollen grains peripheral in the pollinium are tectate-columellate with a relatively thick footlayer (Fig. 1). Pollen in the interior of the pollinium usually lack a tectum; however, the columellae and footlayer are present (Fig. 2). The footlayer is underlain by a thin fibrillar intine (Fig. 2).

EPIDENDROIDEAE
Arethuseae–Bletiinae

Acanthephippium sylhetense Lindl. and *Bletilla striata* (Thunb.) Reichb. f. In both species pollen occurs in tightly packed pollinia. Pollen of *Bletilla striata* appears multiaperturate in the peripheral region of the pollinium, the exine having a number of thin areas (Fig. 3). Pollen wall structure is tectate-columellate (Fig. 4). The columellae are thin and rest on a unilamellar footlayer that is underlain by a thick multilayered intine (Fig. 4). Pollen in the interior of the pollinium lack an exine and are surrounded by intine; however, there appear to be small sporopolleninous granules embedded in the outer portion of the intine (Fig. 5).

→

Figures 1–8. 1, 2. Pollen of the Spiranthoideae.—1. *Sacoila lanceolata*, pollen peripheral in the pollinium showing tectate-columellate wall structure with the well-developed footlayer (FL), ×11,500.—2. *S. lanceolata* pollen interior in the pollinium showing columellae, footlayer, and the thin fibrillar intine. The tectum appears to be absent, ×6,500. 3–8. Pollen of the Epidendroideae.—3. *Bletilla striata* pollen peripheral in the pollinium showing tectate-columellate wall, the thin footlayer, and the thin areas of the exine (arrowheads) that may function as apertures, ×6,500.—4. High magnification of *B. striata* pollen peripheral in the pollinium showing wall structure, ×8,200.—5. Pollen of *B. striata* more interior in the pollinium showing absence of exine, ×8,200.—6. *Acanthephippium sylhetense* pollen peripheral in the pollinium showing tectum, infrastructural layer of oval columellae-like granules that rest on a thin intine. Note the dense nonsporopolleninous substance that coats the entire pollinium (arrowhead), ×3,450.—7. *A. sylhetense* pollen near the periphery of the pollinium showing oval columellae-like granules that rest on the intine (tectum is absent), ×5,300.—8. *A. sylhetense* pollen most interior in the pollinium showing the fibrillar intine. No sporopolleninous wall is present, ×8,200.

Figures 9–16. Pollen of the Epidendroideae.—9. *Coelogyne nitida* pollen peripheral in the pollinium showing the thick tectum and granular infrastructural layer that rests directly on the intine, ×6,500.—10. *C. nitida* pollen interior in the pollinium showing multilayered fibrillar intine. Exine is absent, ×6,500.—11. *Malaxis paludosa* pollinium, ×200.—12. High magnification of *M. paludosa* pollinium showing sporopolleninous outer wall. Note the "sutures" between individual pollen grains (arrowheads), ×2,000.—13. *M. latifolia* pollen peripheral in the pollinium. Note suture between pollen grains (arrowhead, compare to the surface features of *M. paludosa*, Fig. 12), ×3,030.—14. *M. latifolia*, cytoplasm of pollen interior in the pollinium showing the condensed rough endoplasmic reticulum, a structure often found in resting cells of animals, but rare in plants, ×37,770.—15. *M. paludosa* pollen peripheral in the pollinium showing atectate wall, ×7,000.—16. *M. unifolia*, pollen peripheral in the pollinium showing atectate wall, ×7,000.

Figures 17–24. Pollen of the Epidendroideae.—17. Pollen peripheral in the pollinium of *Cattleya skinneri* showing oval columellae-like structures that rest on a thin intine, ×15,125.—18. Pollen interior in the pollinium of *C. skinneri* showing exineless pollen. Note small sporopolleninous granules embedded in the outer layer of the intine (arrowheads), ×12,075.—19. Pollen peripheral in the pollinium of *Encyclia cochleata* showing the thick tectum, and the granular layer that rests directly on the intine. Note the thinning of the tectum (arrowhead) that may act as an aperture, ×20,500.—20. Pollen from the interior of the pollinium of *E. cochleata* showing fibrillar intine; often sporopolleninous granules (arrows) are embedded in this wall layer at the juncture of three or more pollen grains, ×6,500.—21. Pollen peripheral in the pollinium of *Epidendrum anceps* showing the tectum and the granular layer that rests directly on the thick intine. Note the thinning of the tectum (arrowhead), ×11,200.—22. Pollen interior in the pollinium of *E. anceps* showing exineless pollen. Note the minute sporopolleninous granules between pollen grains, ×4,150.—23. *Laelia autumnalis* pollen peripheral in the pollinium showing the tectum on the outermost wall and the granular infrastructural layer that rests on a multilayered intine, ×4,800.—24. Pollen interior in the pollinium of *L. autumnalis* showing exineless pollen with a multilayered intine. Note cytoplasmic connection between adjacent pollen grains (arrow) and minute granules (arrowheads), ×3,500.

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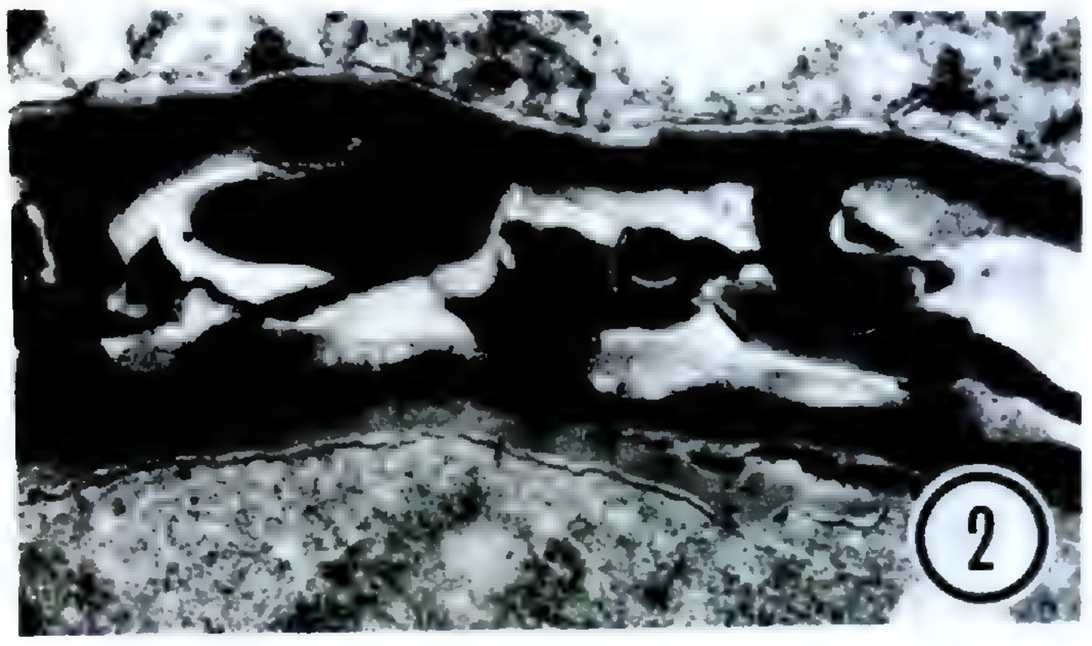
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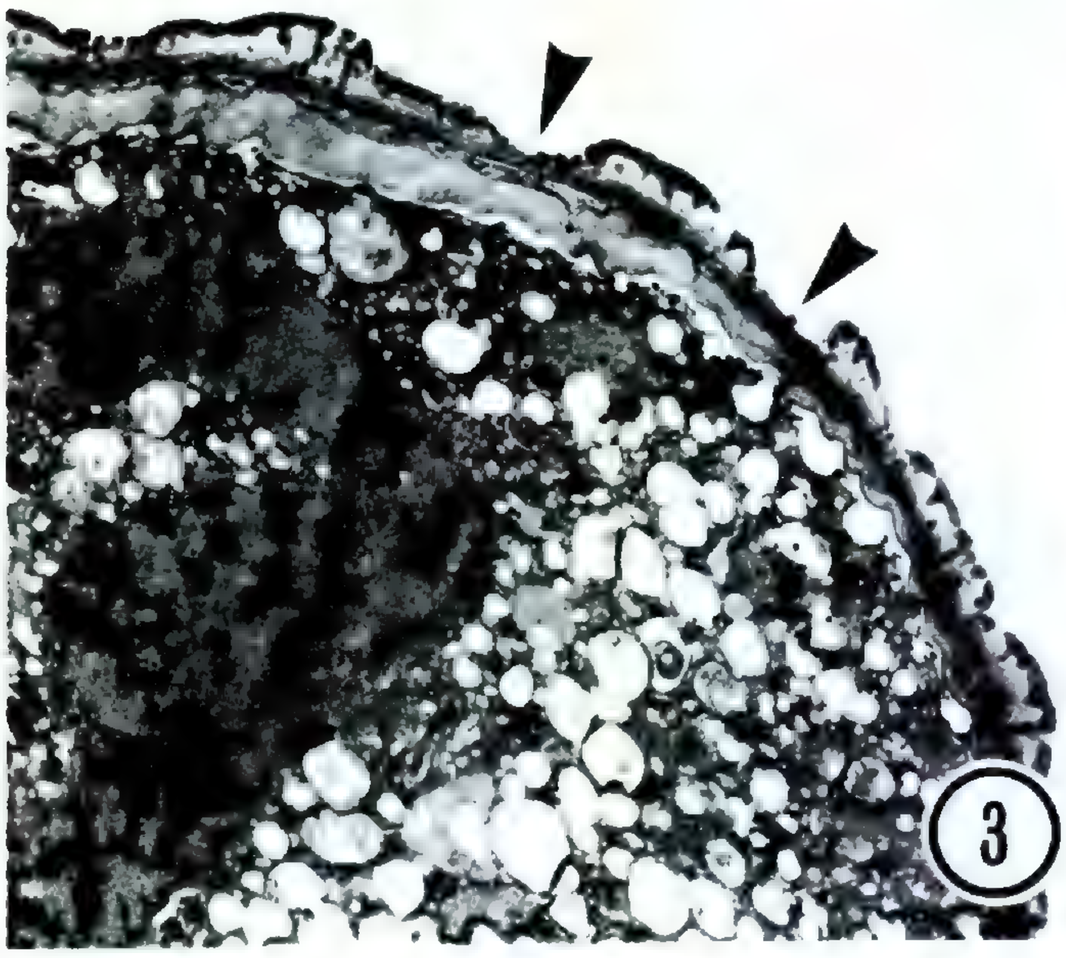
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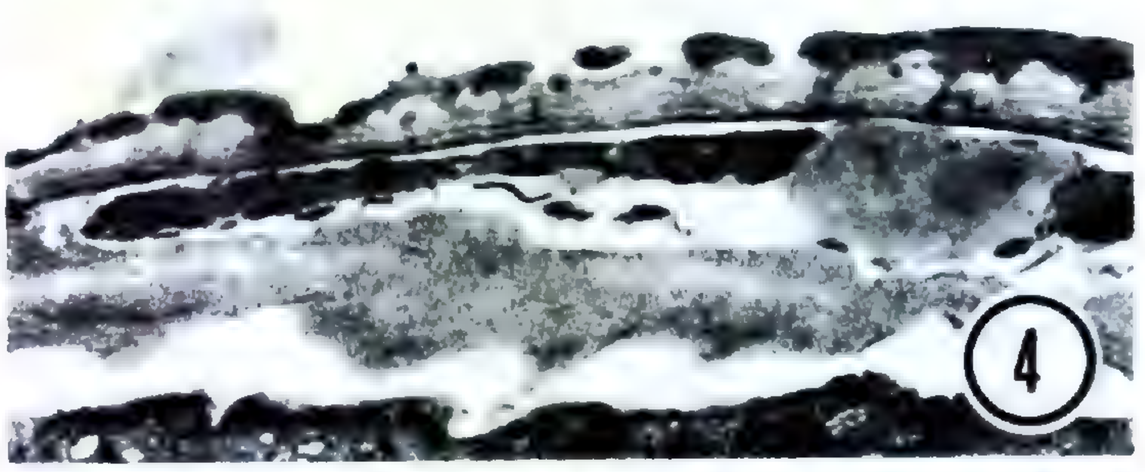
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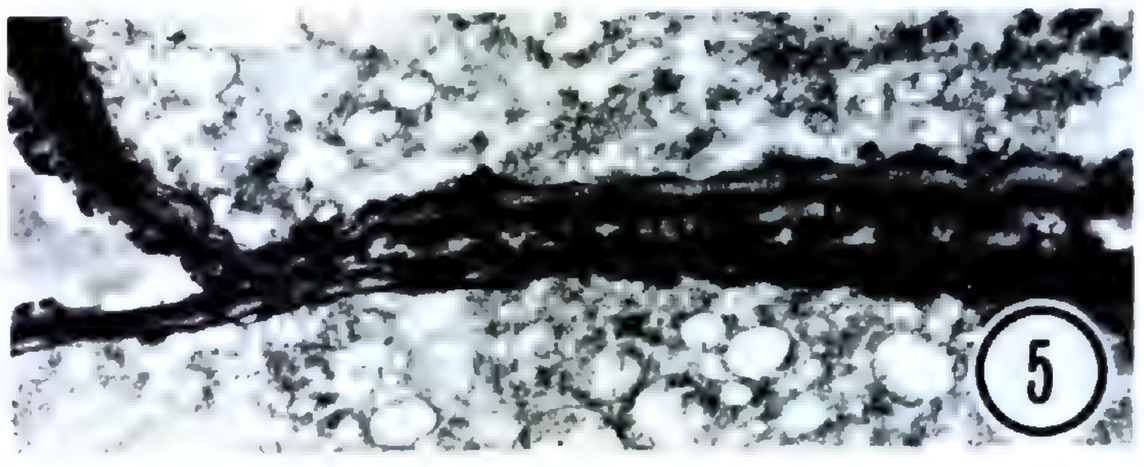
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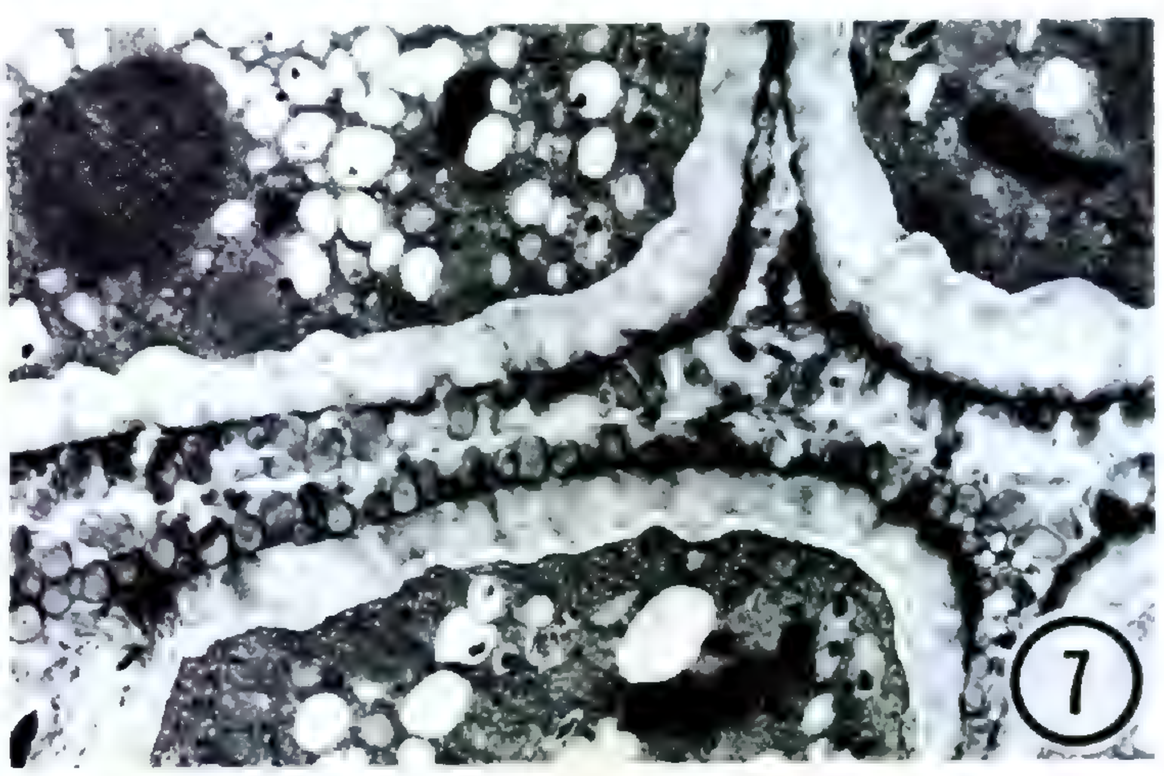
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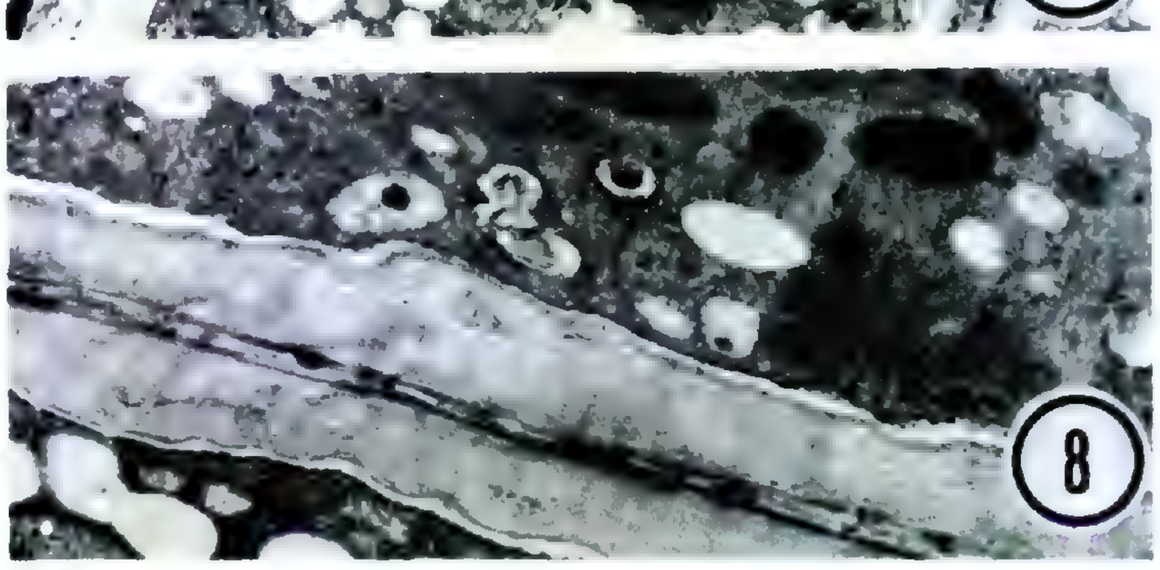
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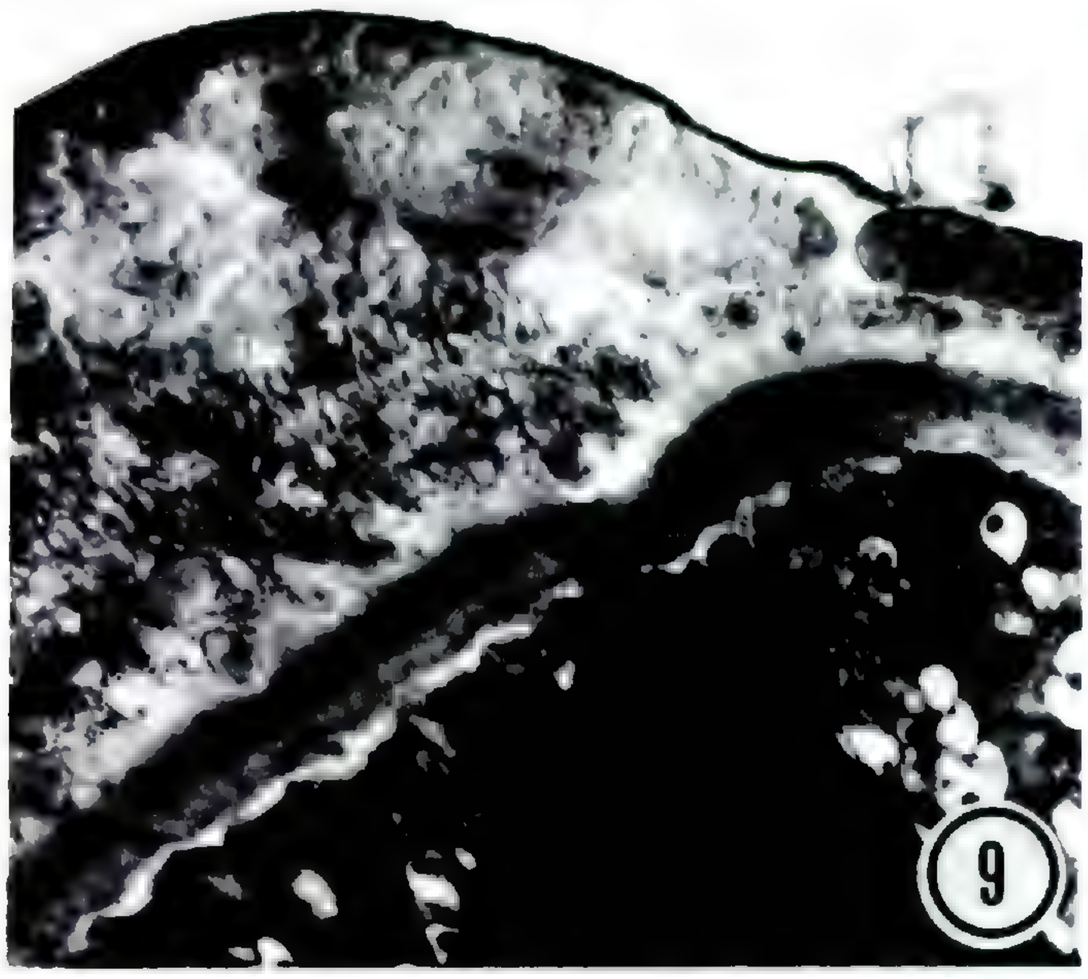
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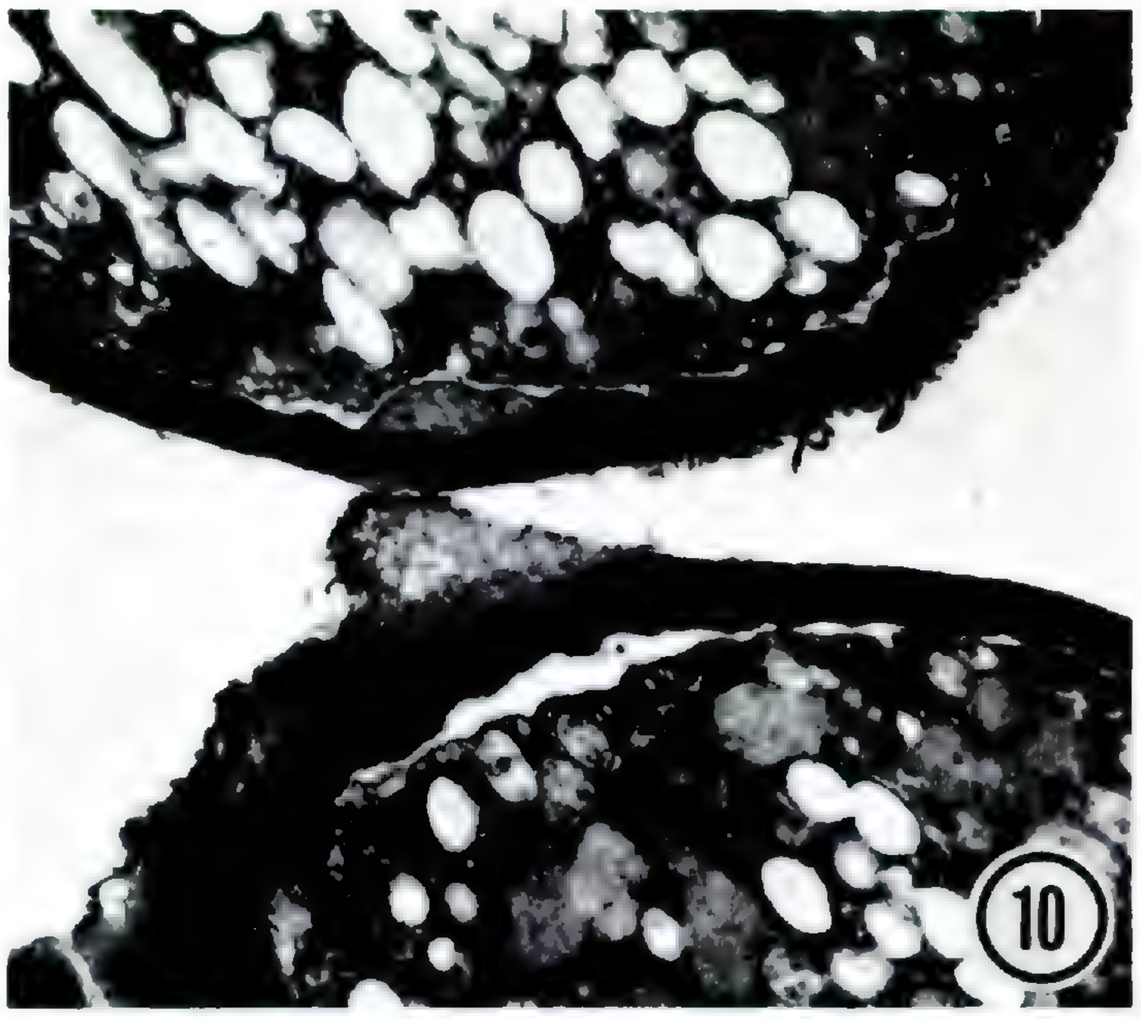
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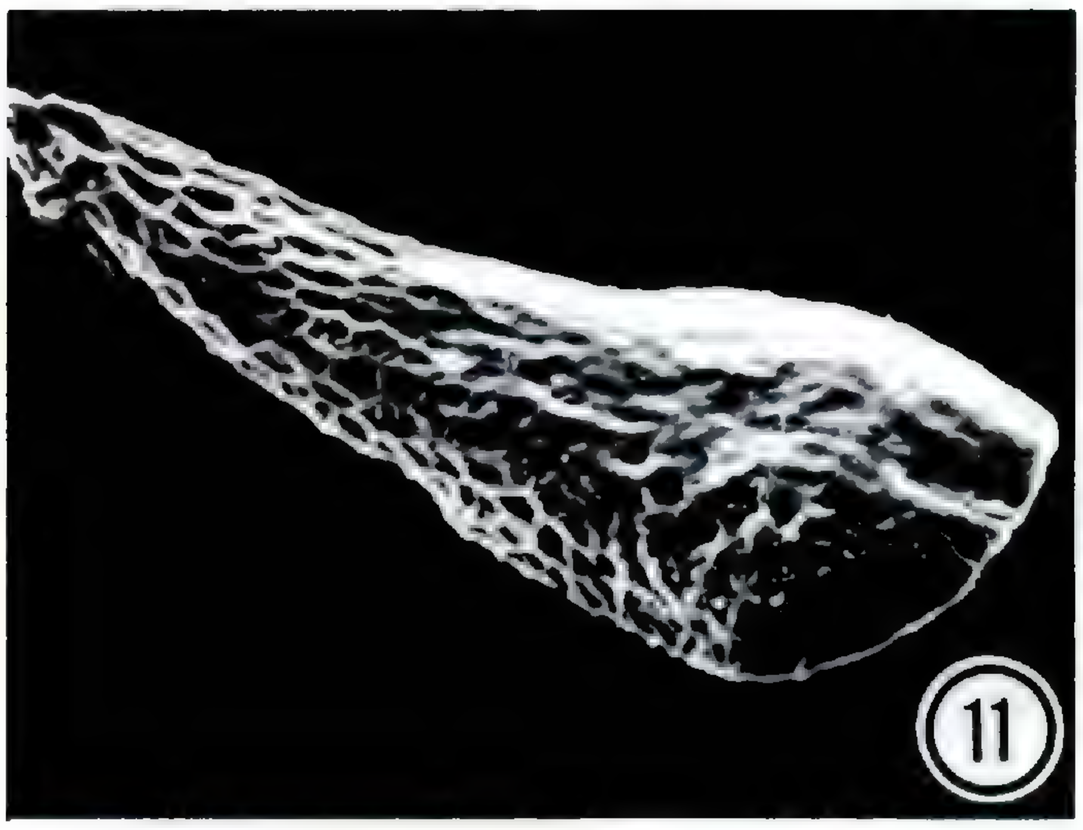
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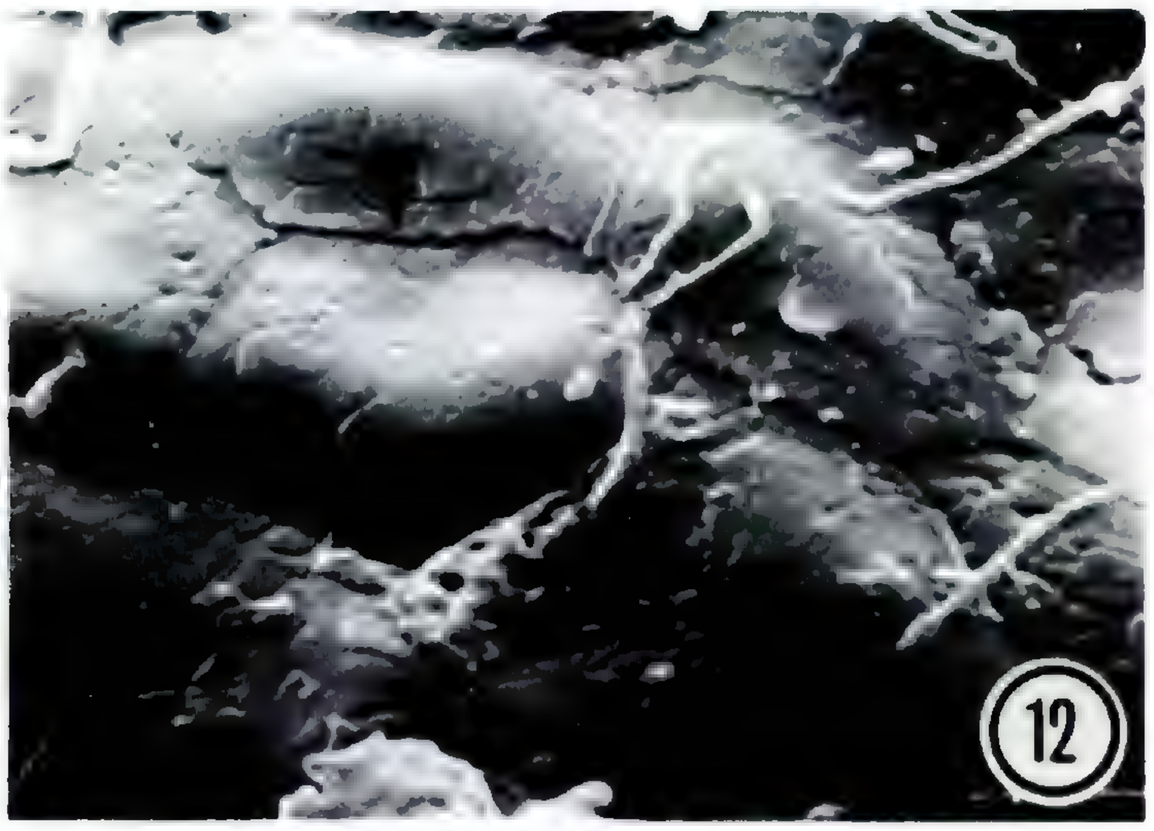
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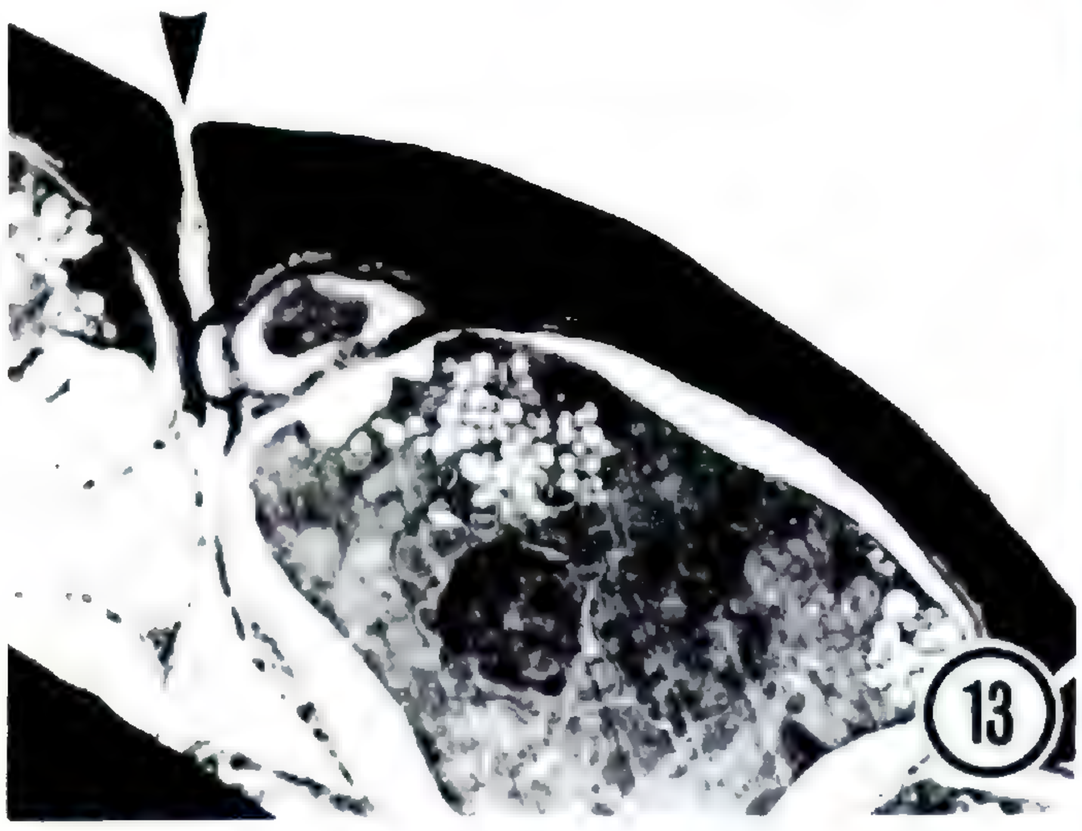
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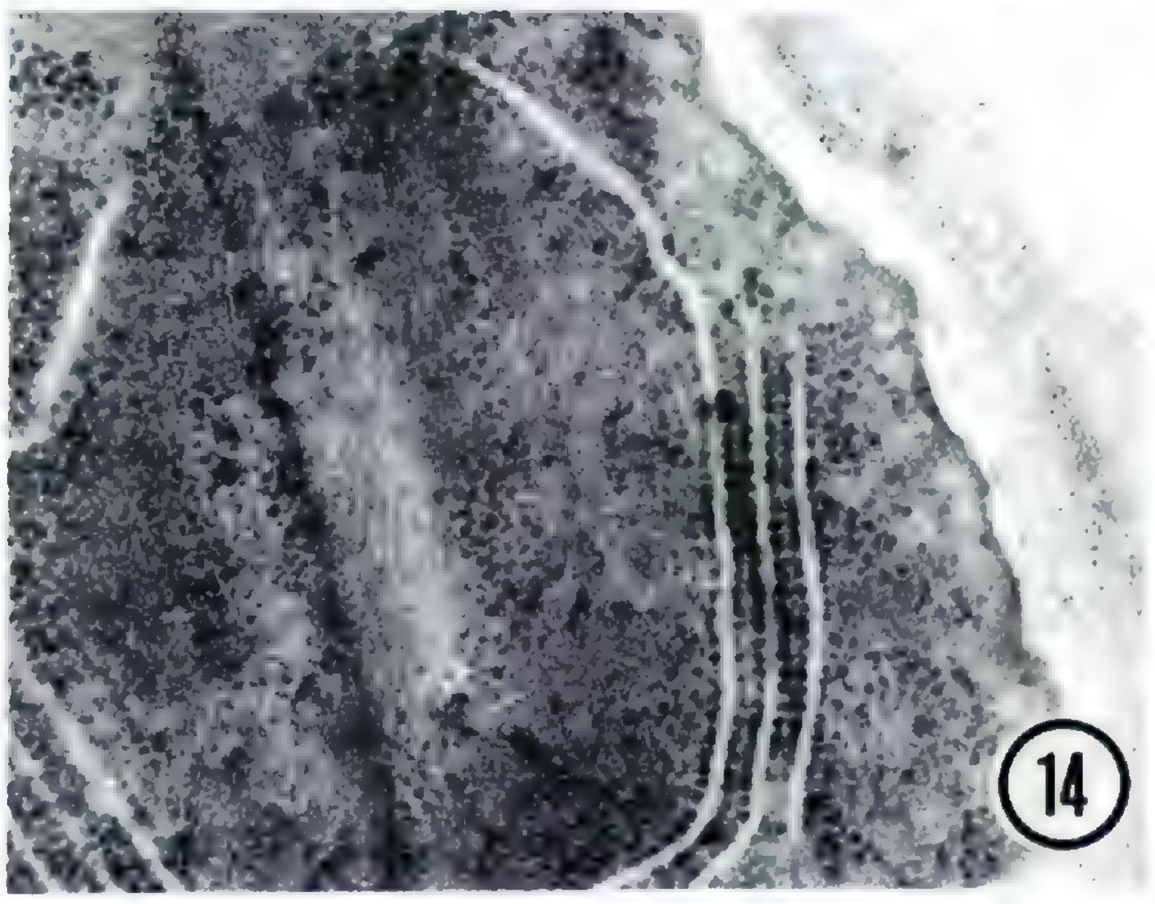
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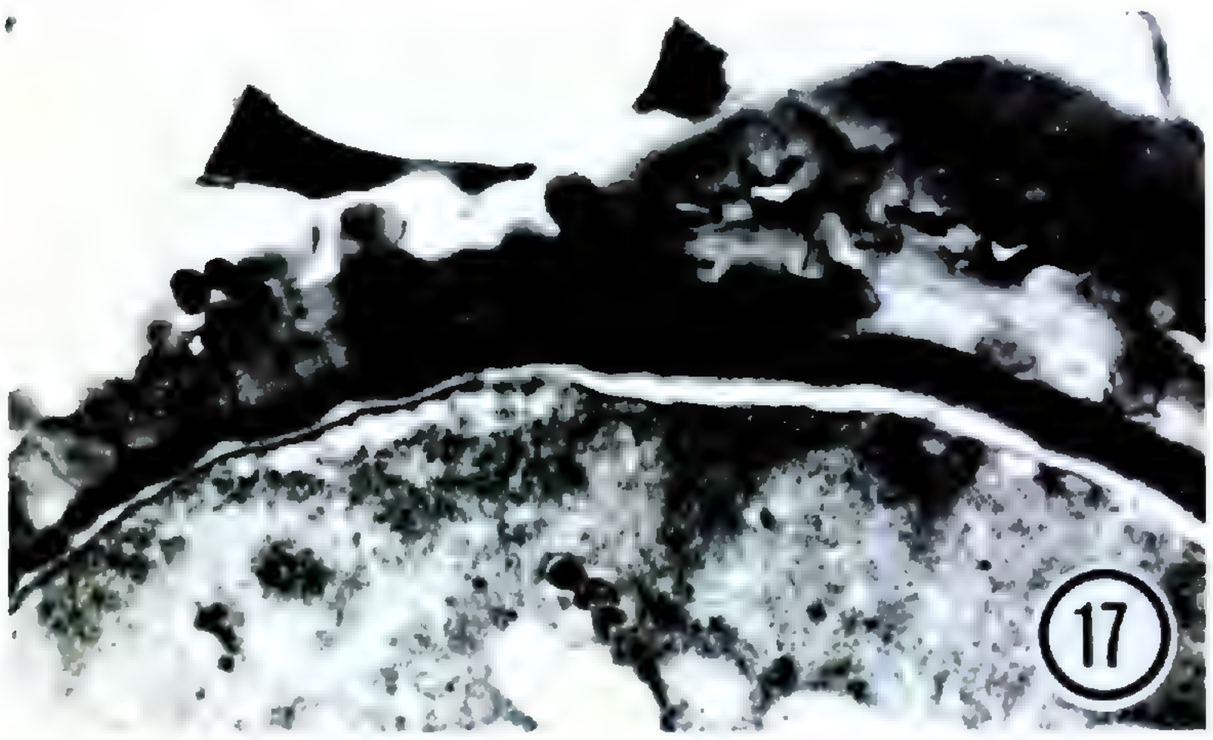
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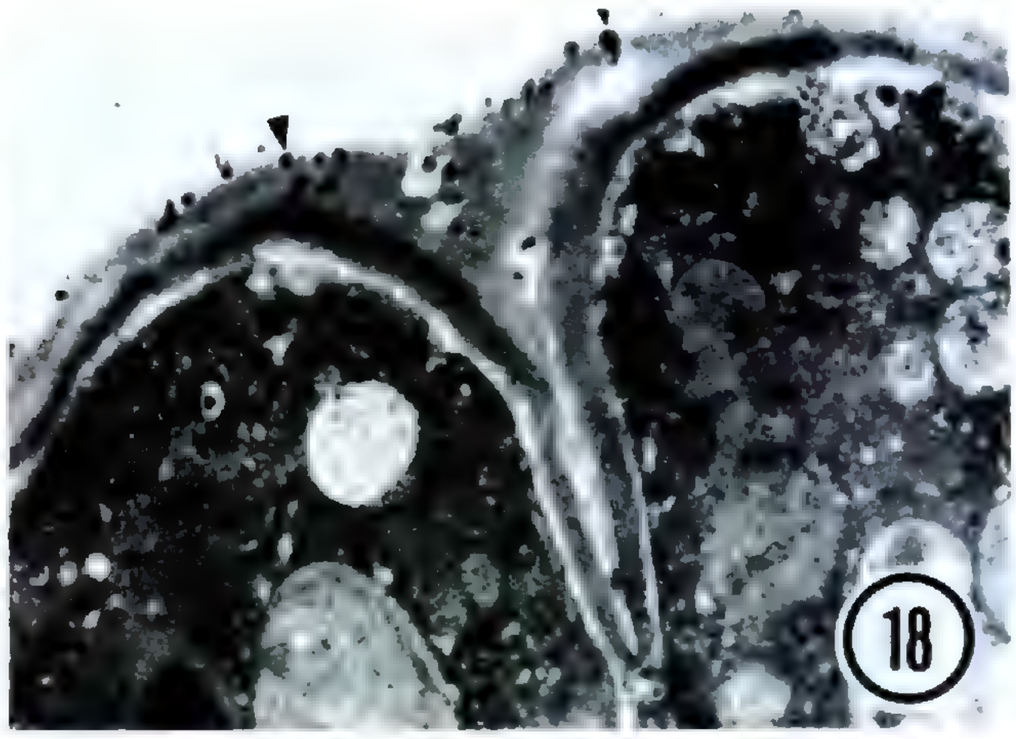
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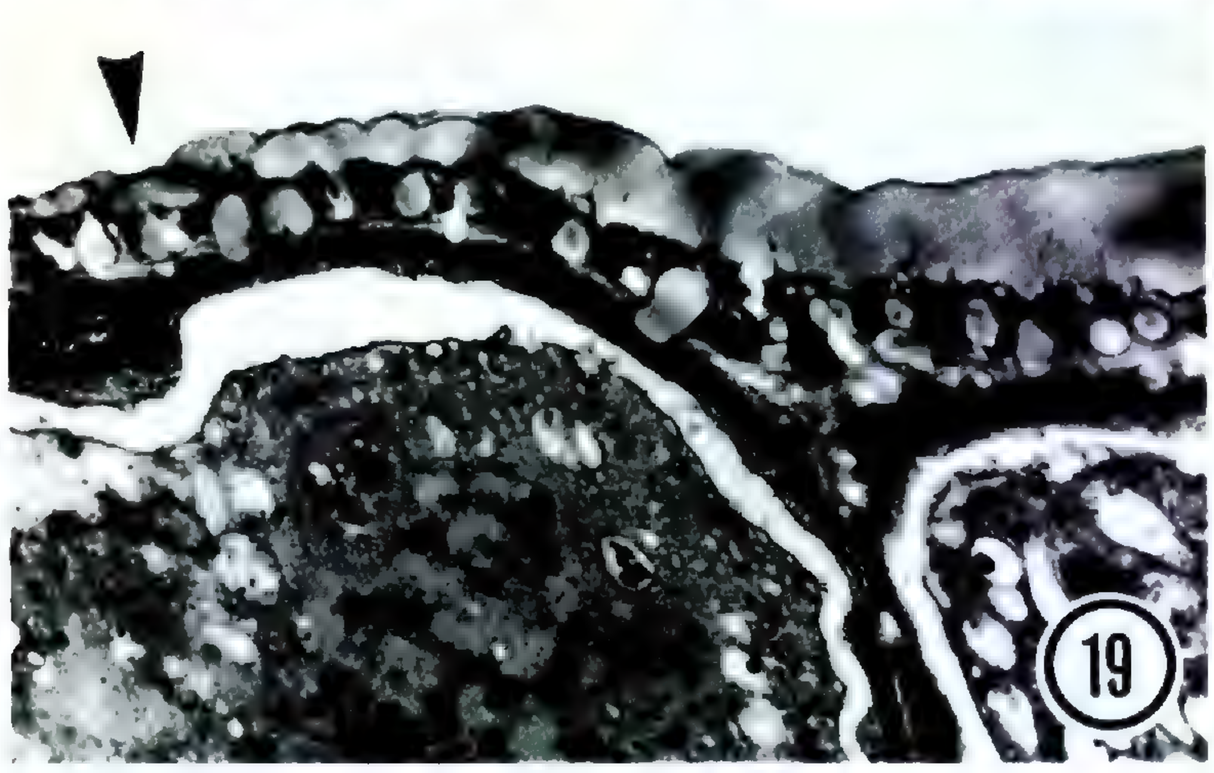
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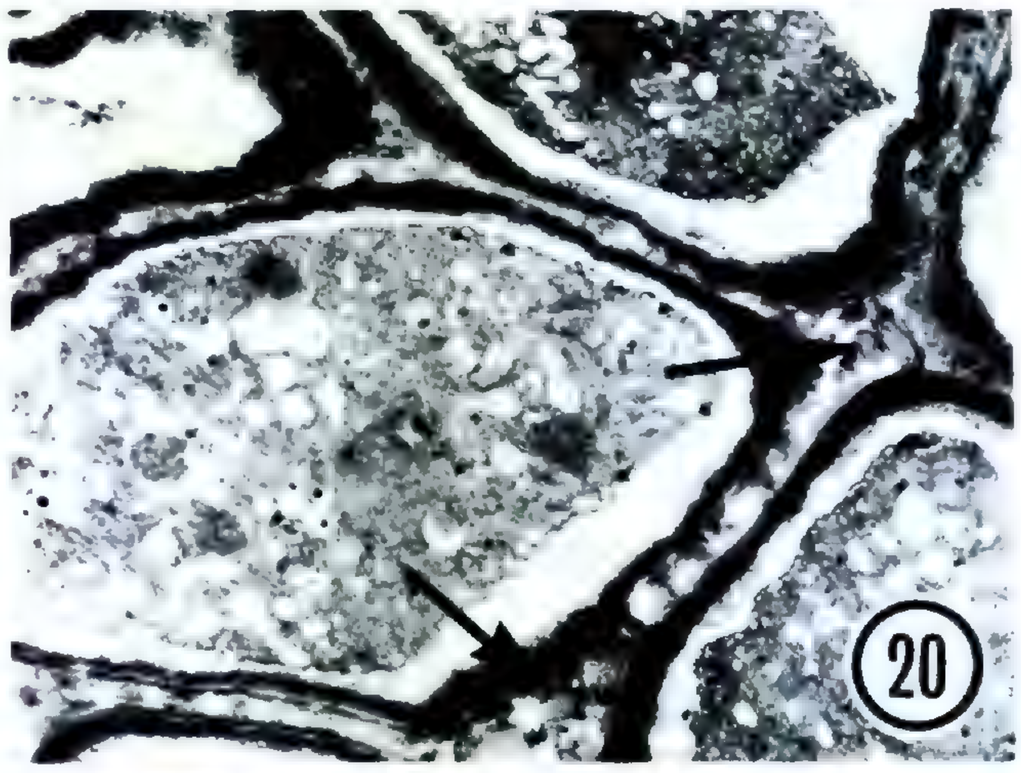
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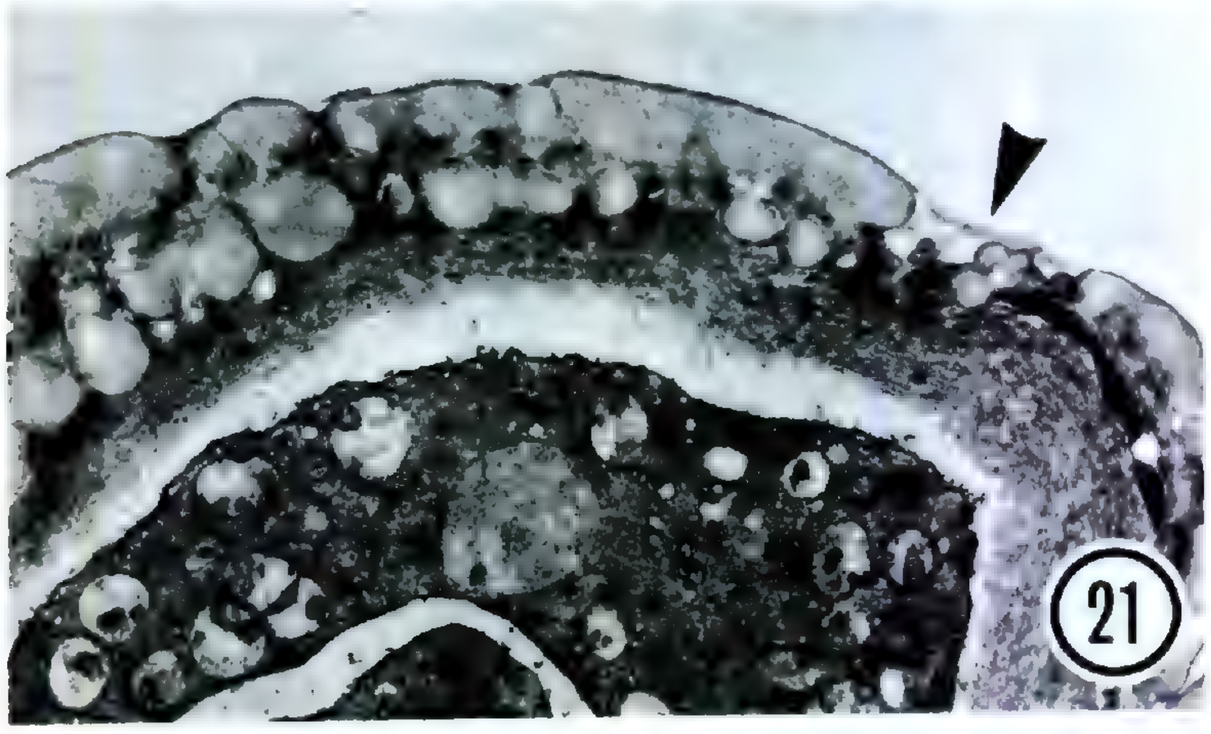
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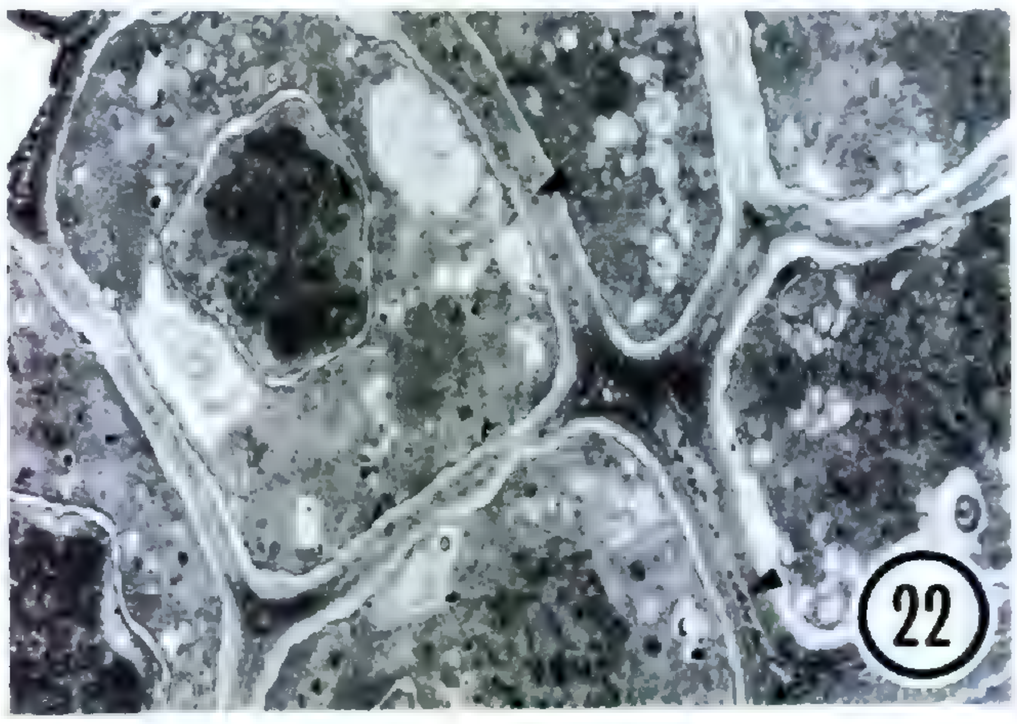
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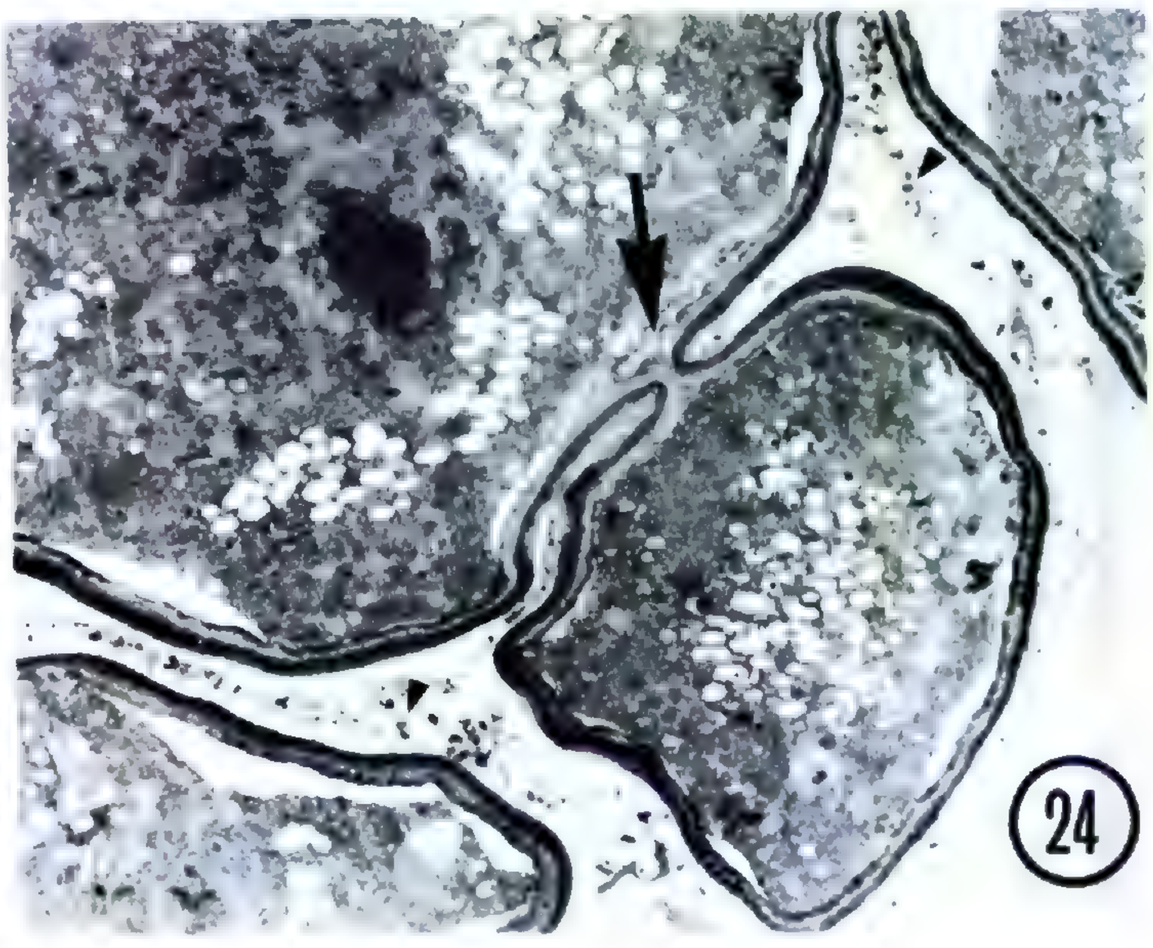
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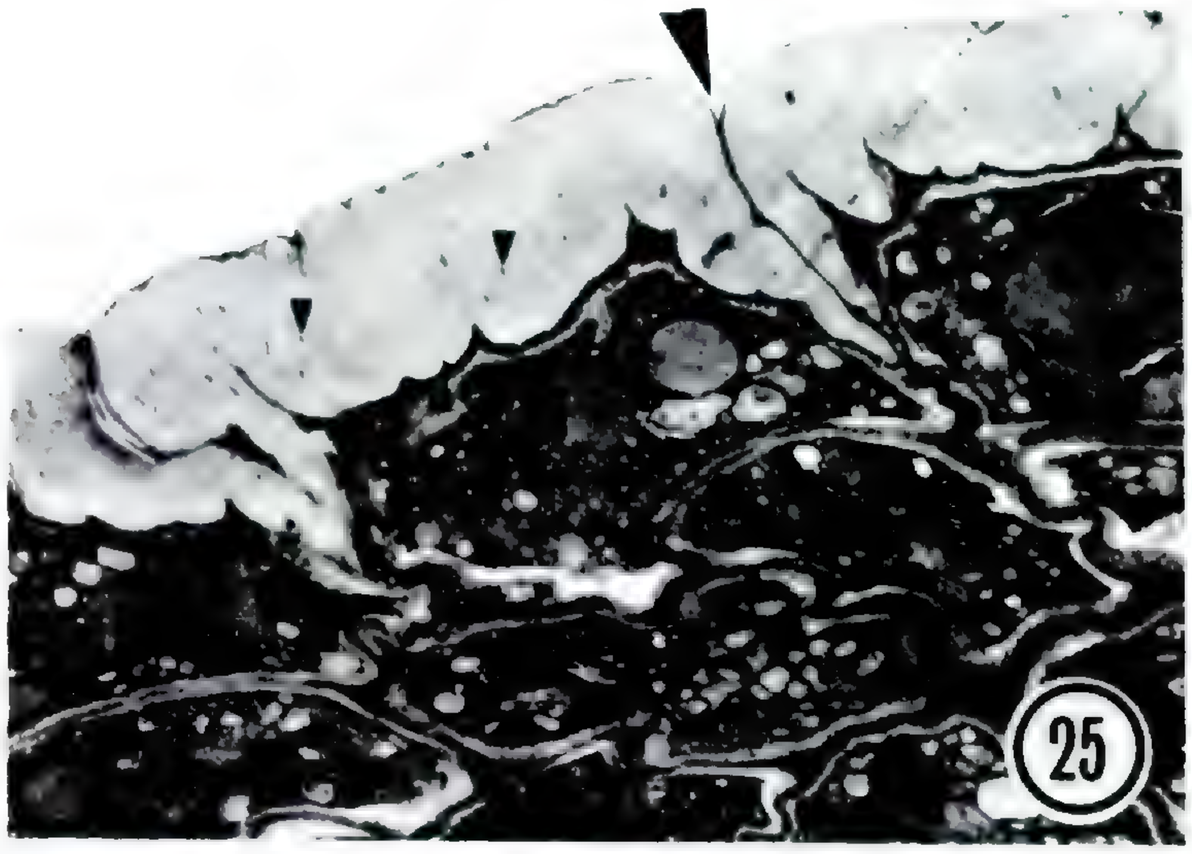
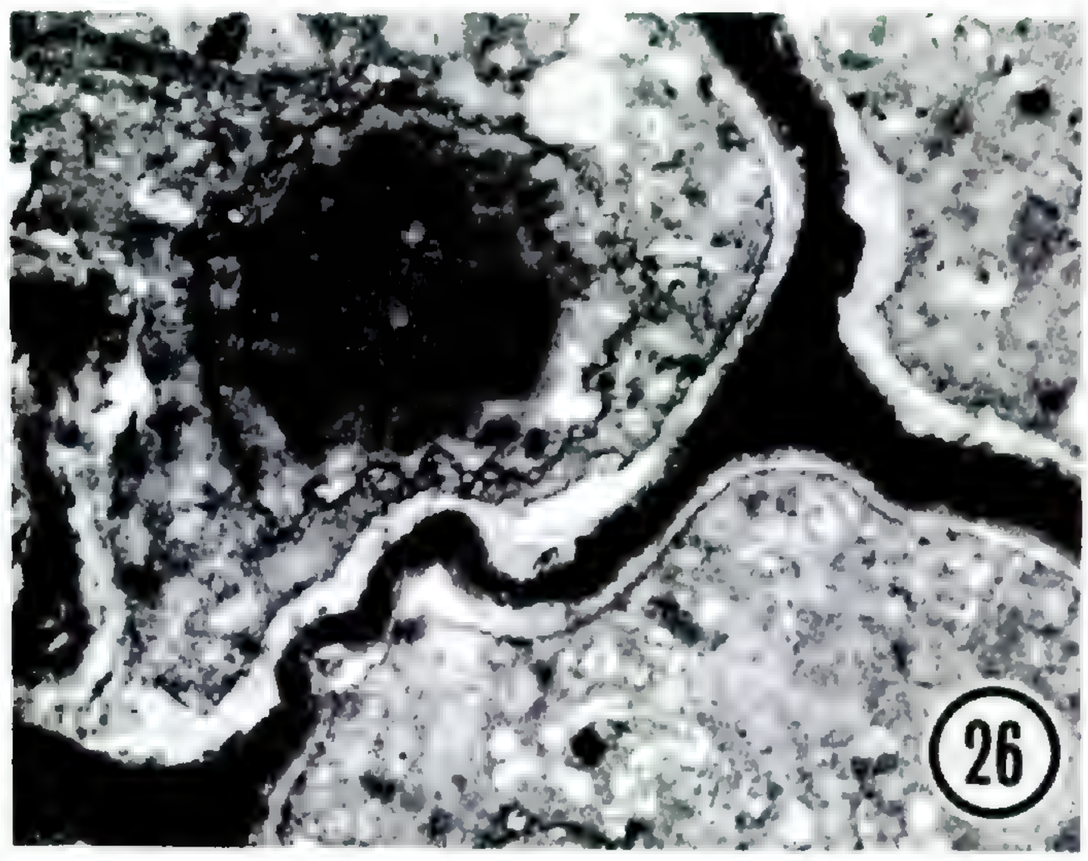
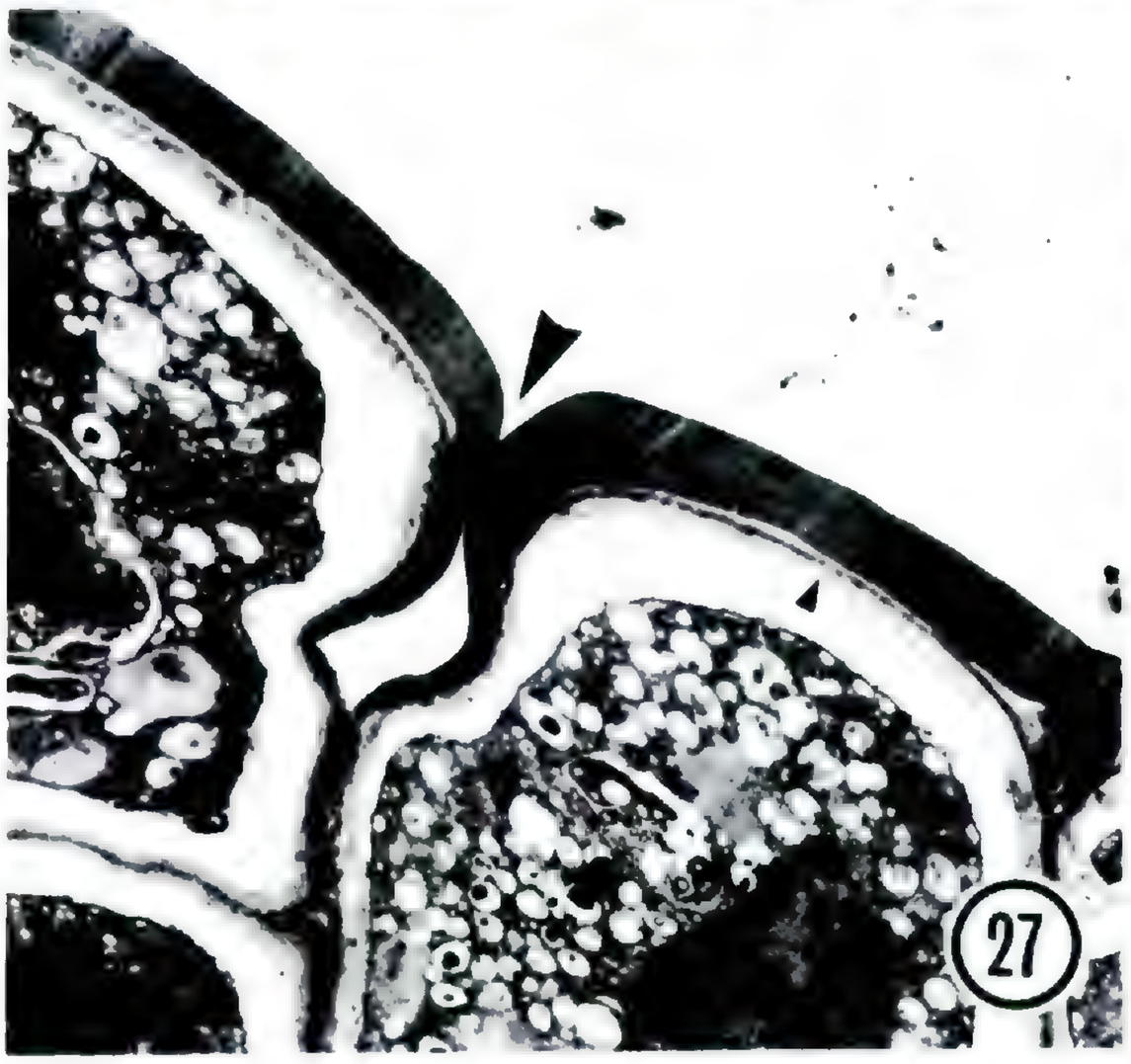
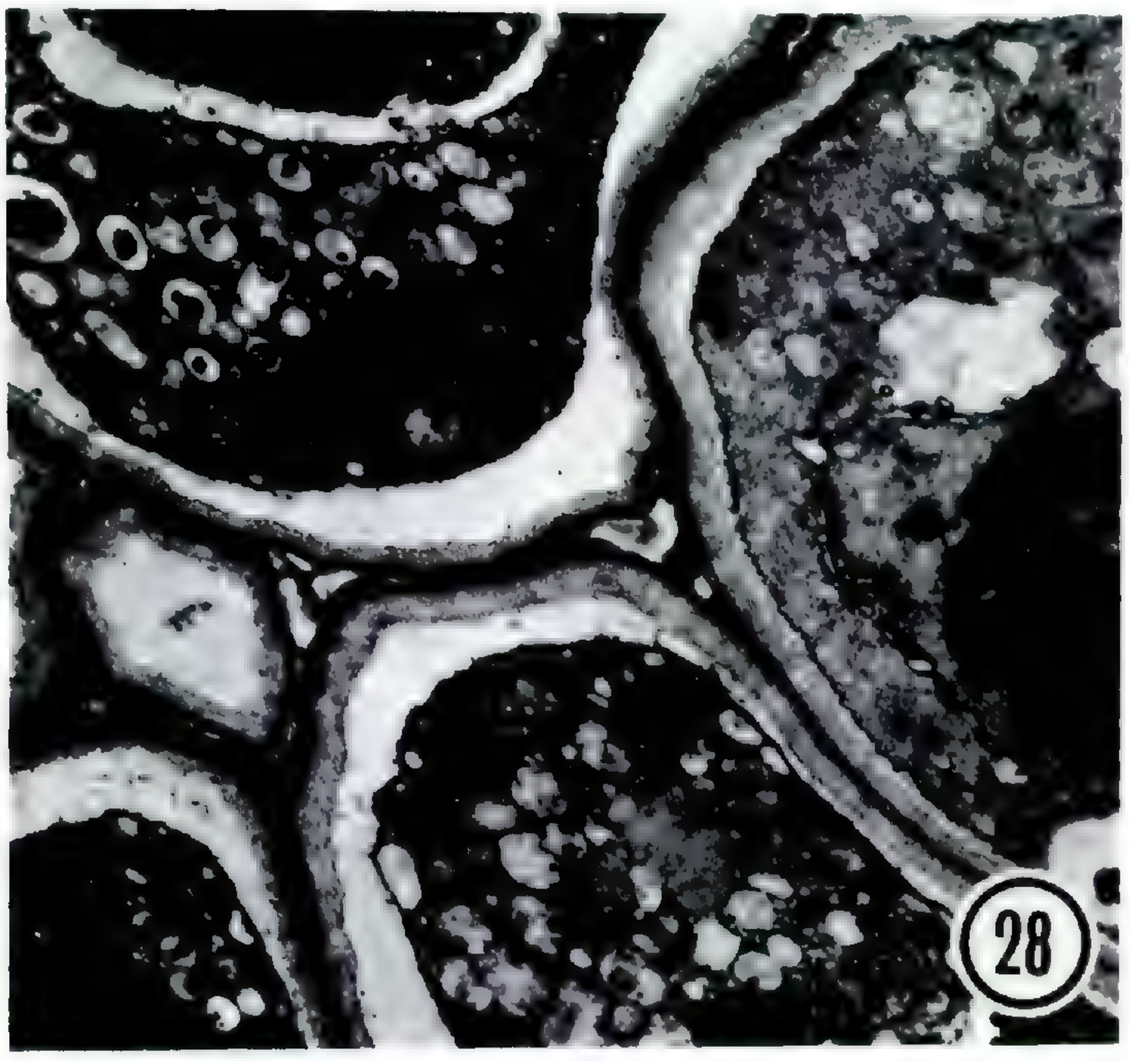
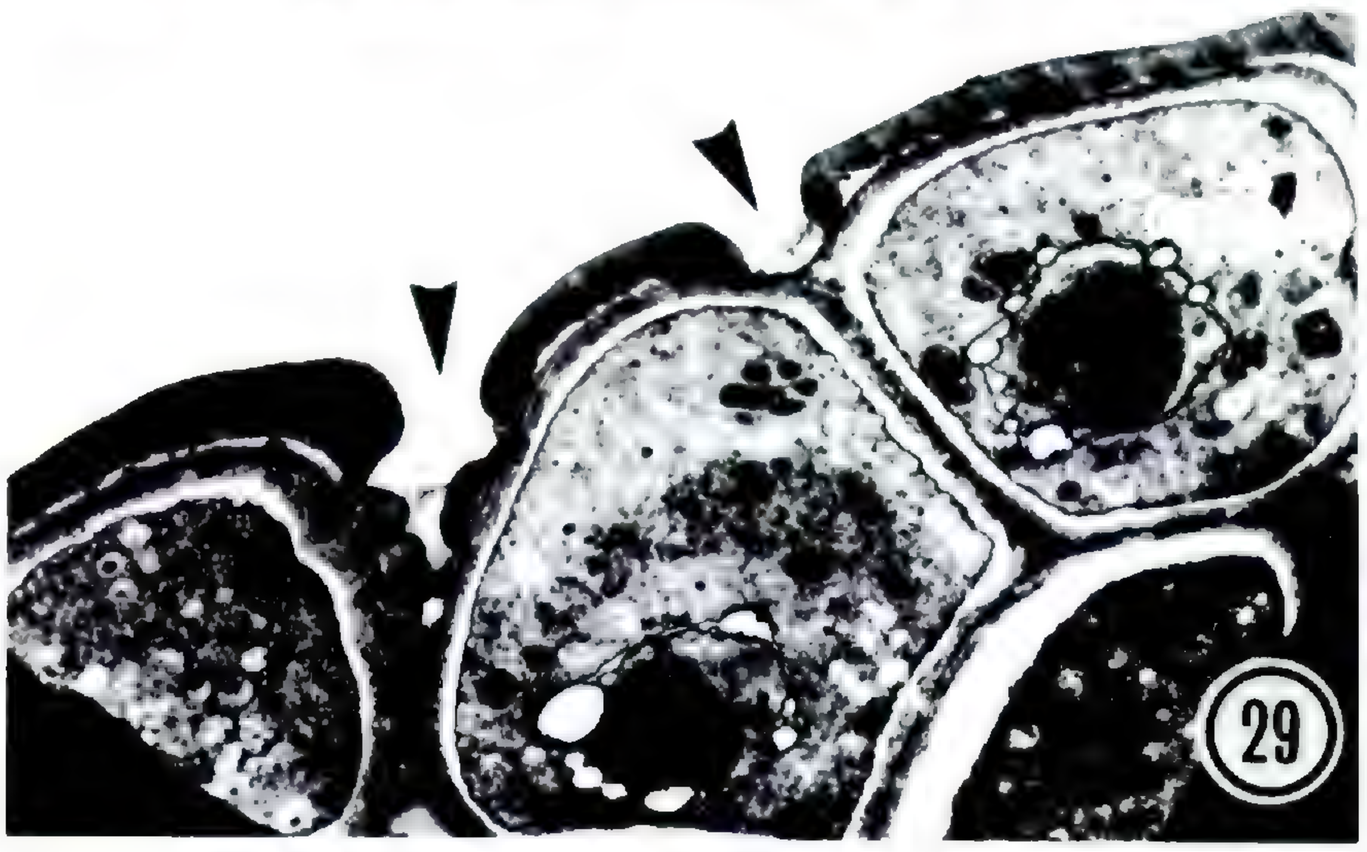
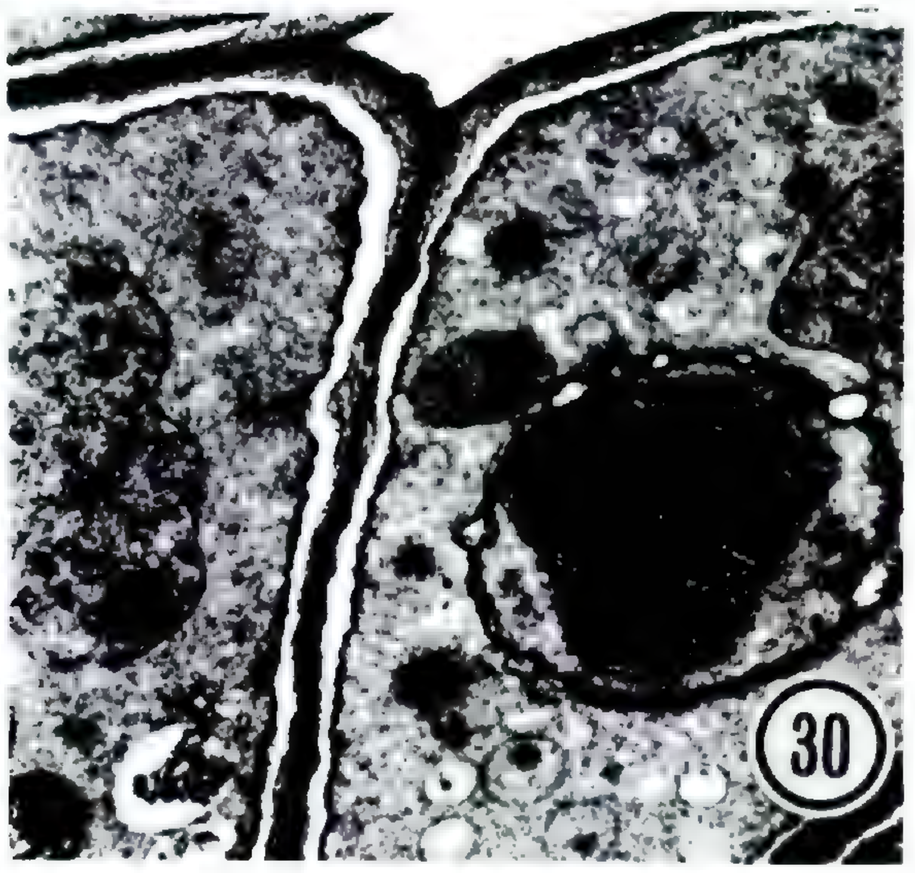












FIGURES 25–30. Pollen of the Epidendroideae.—25. Pollen peripheral in the pollinium of *Masdevallia caudata* showing thick atectate exine that is underlain by a thin intine. Note the microchannels that traverse the lower portion of the exine (small arrowheads) and the "suture" between adjacent pollen grains (large arrowhead), ×5,300.—26. Pollen interior in the pollinium of *M. caudata* showing exineless pollen grains that are surrounded by a thin intine. The dense nonacetolysis resistant layer between pollen grains may be part of the intine, ×10,000.—27. Pollen peripheral in the pollinium of *Dryadella edwallii* showing atectate exine with thin bilayered intine (small arrowhead). Note suture between adjacent pollen grains. When the tectum of adjacent pollen grains is closely appressed to one another the exine may prevent dessication of the exineless interior pollen grains. As the pollinium expands these sutures may open permitting the emergence of the pollen tubes (also see Figs. 15, 16, 25, 29), ×6,500.—28. Pollen interior in the pollinium of *D. edwallii* showing multilayered intine, ×10,000.—29. Pollen peripheral in the pollinium of *Pleurothallis janetiae* showing atectate exine. Note the suture between adjacent pollen grains (arrowheads), ×5,800.—30. Pollen interior in the pollinium of *P. janetiae* showing the presence of only the intine, ×10,500.

Acanthephippium sylhetense pollen grains are inaperturate. Exine sculpturing is psilate. The wall structure of pollen peripheral in the pollinium is tectate with oval columellae-like elements in the infrastructure (Fig. 6). The closely spaced columellae-like elements are often thick branching rods to oval and granular-like structures that support the tectum (Fig. 6). The bases of the columellae rest directly on a thin fibrillar intine. In the interior of the pollinium the tectum is generally absent, being comprised of short, stout columellae or irregularly shaped granules (Fig. 7). The exine is entirely absent from the innermost pollen in the pollinia; each pollen grain is surrounded by a fibrillar intine (Fig. 8).

Coelogyneae–Coelogyninae

Coelogyne nitida Lindl. Pollen occurs in tightly packed pollinia and appears inaperturate. Pollen peripheral in the pollinium have a thick tectum, which is underlain by a massive granular layer (Fig. 9). The granular layer rests directly on a thick bilayered intine (Fig. 9). Pollen interior in the pollinium lack an exine, and each pollen grain is surrounded by a bilayered intine (Fig. 10).

Malaxideae

Malaxis latifolia J. E. Sm., *M. paludosa* Sw., and *M. unifolia* Michx. Pollen occurs in small, tightly packed pollinia and are inaperturate (Figs. 11, 12). The outer wall of pollen peripheral in the pollinium is thick and homogeneous (atectate) (Figs. 13, 15, 16). Each pollen grain peripheral in the pollinium has its own wall (Figs. 12, 13); however, the walls are closely appressed to one another, often giving the appearance that the entire pollinium is enclosed by a single sporopolleninous wall. Pollen interior to these outermost pollen grains appear to lack exine in *M. latifolia* (Fig. 13) and are surrounded only by intine; however, a thin homogeneous sporopolleninous wall surrounds each microspore in the two North American species (Figs. 15, 16). All three species investigated are identical with regard to wall ultrastructure of pollen most peripheral in the pollinium. The cytoplasm in *M. latifolia* has what appears to be condensed rough endoplasmic reticulum (Fig. 14), a condition often found in resting cells in animals, but a rare occurrence in plants.

Epidendreae–Laeliinae

Cattleya skinneri Batem., *Encyclia cochleata* (L.) Lemee, *Epidendrum anceps* Jacq., and *Laelia autumnalis* Lindl. Pollen in all four taxa occur in tightly packed pollinia. Pollen grains peripheral in the pollinium have a thick tectum underlain by large, stout columellae or oval granules that rest directly on the intine (Figs. 17, 19, 21). Pollen more interior in the pollinium are exineless and surrounded only by an intine (Figs. 18, 20, 22). However, at the junctures of two or more pollen grains, sporopolleninous granules are evident (*Cattleya*, Fig. 18 and *Encyclia*, Fig. 20). In *Epidendrum* (Fig. 22) minute sporopolleninous granules are embedded in the intine between adjacent pollen grains.

Laelia autumnalis deviates from the above taxa by the occurrence of the tectate-granular wall. Pollen grains peripheral in the pollinium have a thick tectum underlain by a granular layer (Fig. 23). The tectum peters out on the lateral faces of the peripheral pollen grains (Fig. 23). Pollen in the interior of the pollinium are similar to *Epidendrum* in having minute sporopolleninous granules embedded in the outer layer of the intine (Fig. 24).

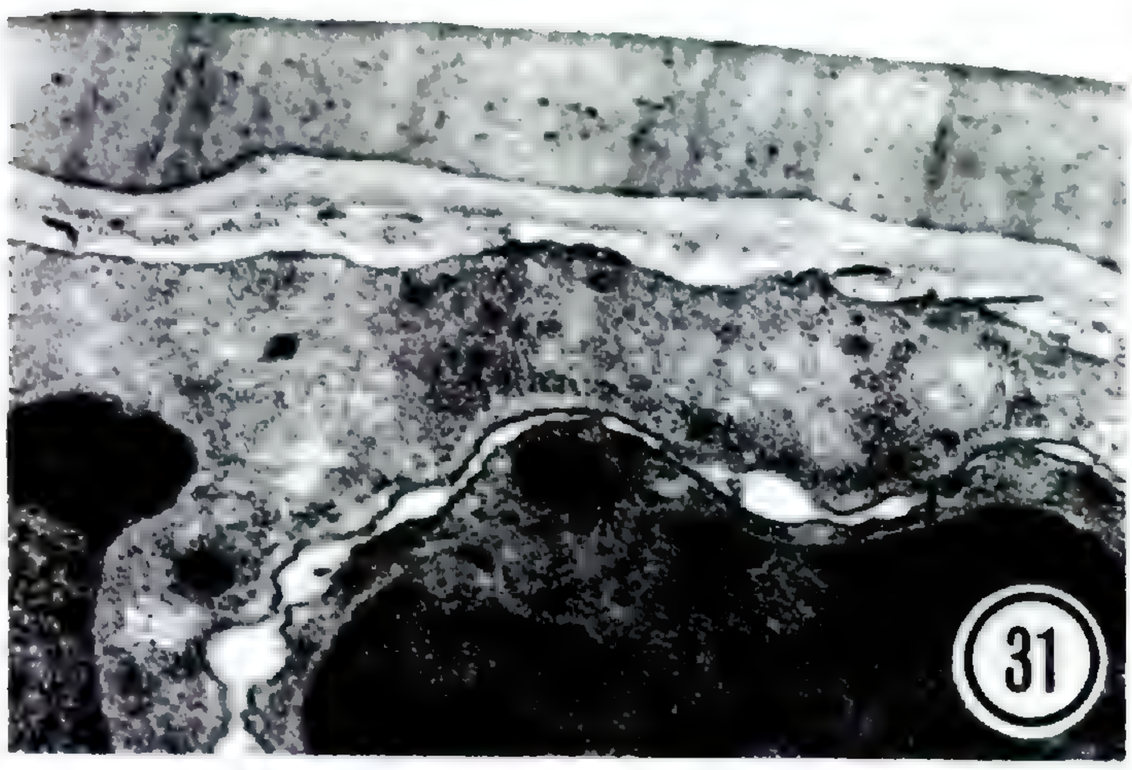
Epidendreae–Pleurothallidinae

Pollen of all four taxa investigated in this subtribe occur in tightly packed pollinia and are inaperturate.

Masdevallia caudata Lindl. Pollen grains peripheral in the pollinia have a thick homogeneous outer layer (Fig. 25). The inner portion of the exine is also homogeneous but is traversed by minute channels (Fig. 25). The inner surface of the exine is endo-rugulate and rests directly on a thin intine (Fig. 25). Pollen in the interior of the pollinium are exineless, surrounded only by the intine (Fig. 26).

Dryadella edwallii (Cogn.) Luer. The wall structure of pollen most peripheral in the pollinium consists of a thick homogeneous wall (atectate) (Fig. 27). This wall layer rests directly on a thin intine. Pollen grains in the interior of the pollinium are exineless and are surrounded by a multilayered intine (Fig. 28).

Pleurothallis janetiae Luer and *Restrepia striata* Rolfe. Both taxa have similar wall structure and will be treated together. Pollen grains peripheral in the pollinium have a thick homogeneous tectum (atectate) that rests directly on the intine (Figs. 29, 31). However, the exine becomes rugulate (the rugulae are large granular structures) on the lateral walls of the outer pollen grains (Fig. 29, 32). Pollen interior in the pollinium lack exine and are sur-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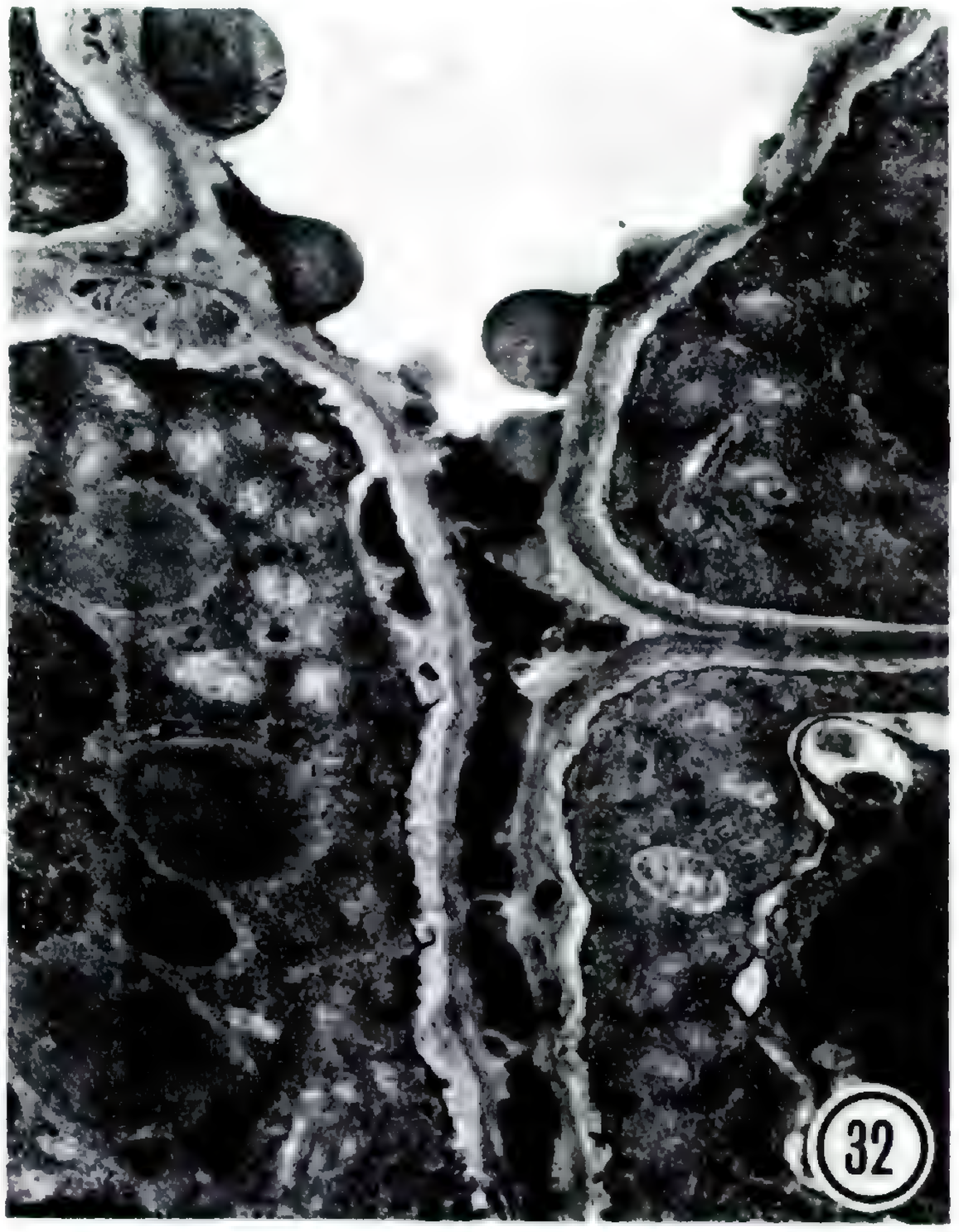
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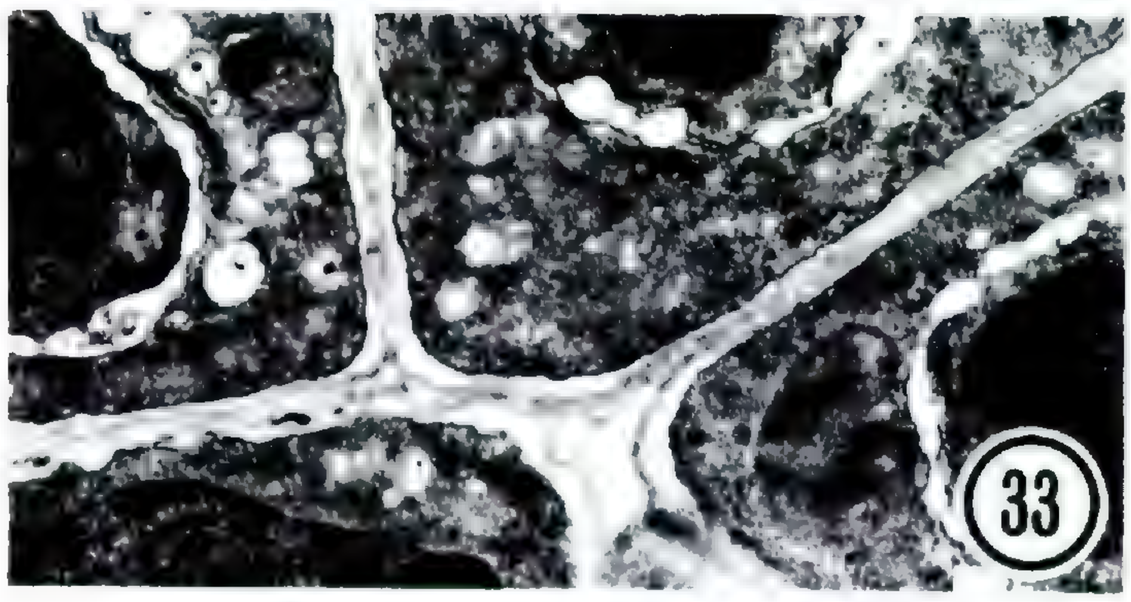
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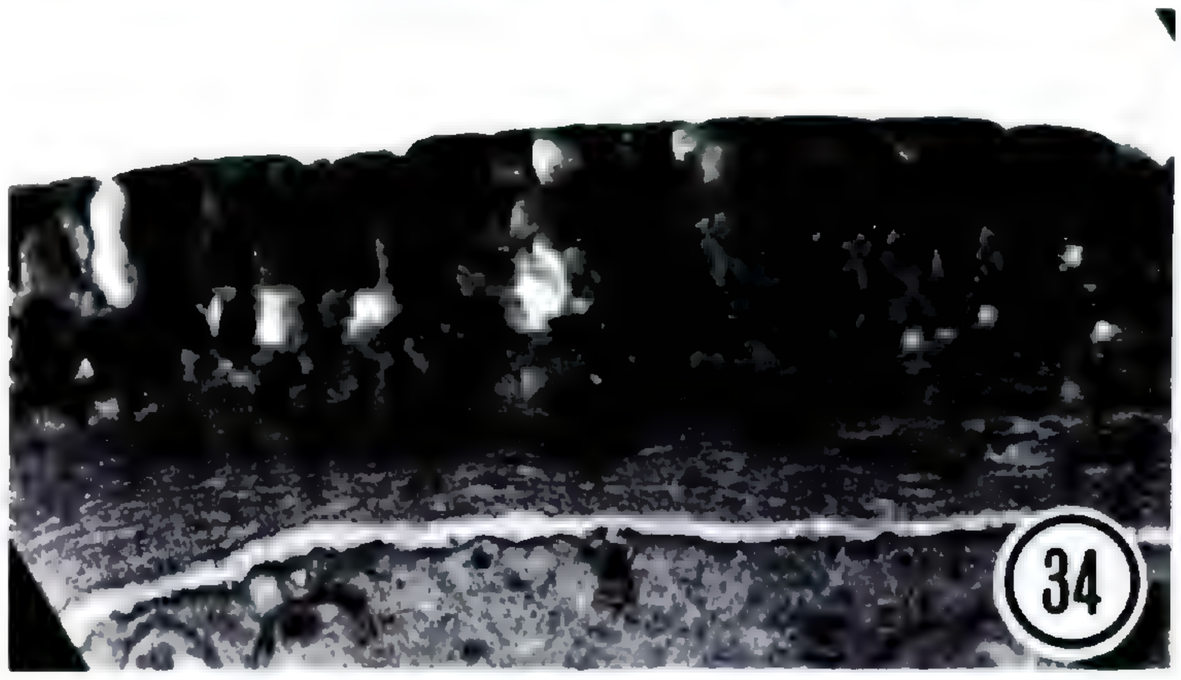
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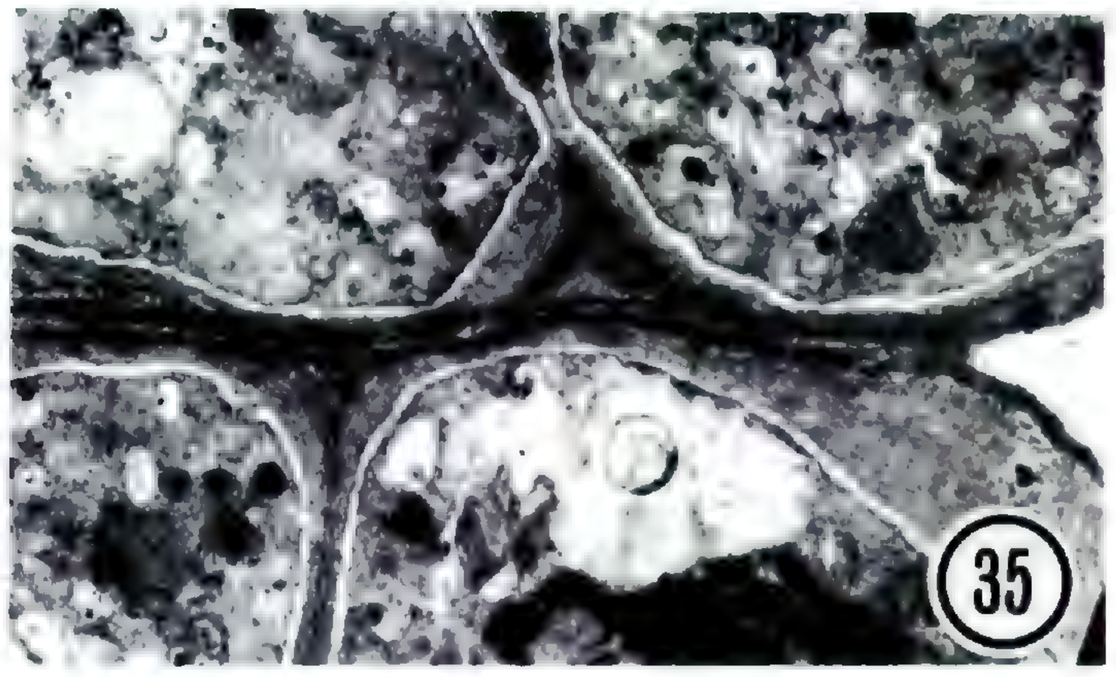
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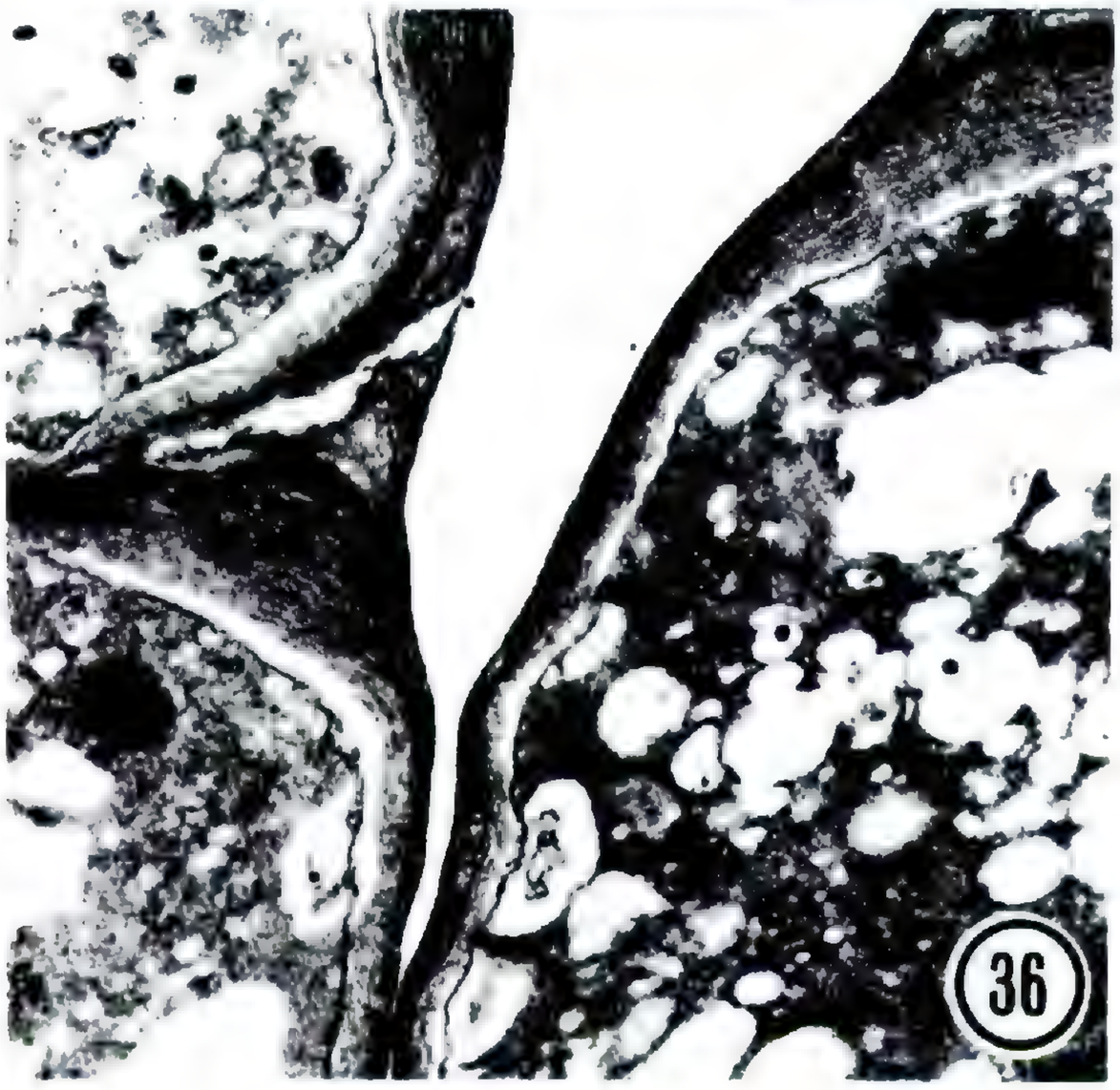
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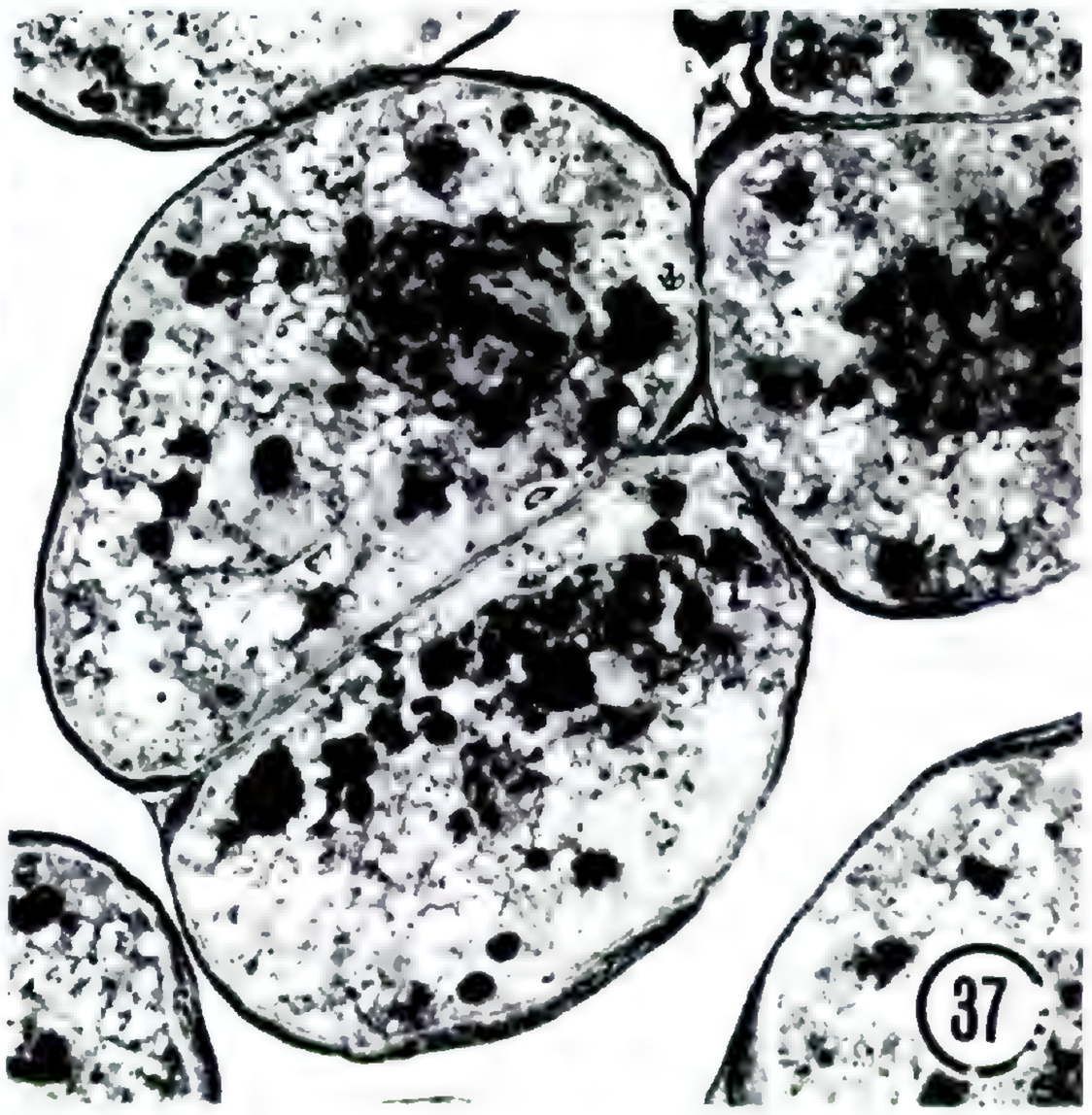
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rounded only by a multilayered intine (Figs. 30, 33).

Epidendreae–Dendrobiinae

Dendrobium nobile Lindl. Pollen grains occur in tight pollinia and are inaperturate. Grains peripheral in the pollinium have a thick tectum underlain by a granular layer (Fig. 34). The tectum peters out toward the contact areas of adjacent pollen grains, where the granular layer is only present. The granular layer rests on a fibrillar intine (Fig. 34). Pollen interior in the pollinium are exineless and surrounded by a bilayered intine (Fig. 35).

D. aphyllum (Roxb.) Fischer. Pollen grains occur in loosely packed pollinia and are inaperturate. Pollen in both the peripheral and interior regions of the pollinium are exineless (Figs. 36, 37); however, pollen peripheral in the pollinium have a massive multilayered intine (Fig. 36). Pollen in the interior of the pollinium have a thin multilayered intine (Fig. 37).

Epidendreae–Bulbophyllinae

Bulbophyllum imbricatum Lindl. Pollen grains occur in tightly packed pollinia and are inaperturate. Pollen peripheral in the pollinium have a tectate-granular wall (Fig. 38), the granular layer resting directly on a thin intine. Pollen grains interior in the pollinium are exineless, surrounded only by intine (Fig. 38).

Vandeae–Sarcanthinae

Schoenorchis fragrans (Par. & Reichb. f.) Seid. & Smit. Pollen grains occur in tightly packed pollinia and are inaperturate. Pollen peripheral in the pollinium are surrounded by a homogeneous atectate exine (Fig. 39). Pollen interior in the pollinium is exineless, and each pollen grain is surrounded by a thin bilayered intine (Fig. 39).

Ascocentrum ampullaceum (Roxb.) Schltr., *Cleisostoma racemiferum* (Lindl.) Garay, *Haraella retrocalla* (Hayata) Kudo *Luisia teres* (Thunb.). Bl. var. *botanensis* (Fuk.) T. P. Lin, *Phalaenopsis lueddemanniana* Reichb. f., *Thrixspermum saruwatarii* (Hayata) Schltr. Pollen grains of all the species investigated occur in tightly packed pollinia. Pollen peripheral in the pollinia have a thick homogeneous, atectate wall with endo-rugulations (*Ascocentrum*, Fig. 46; *Phalaenopsis*, Fig. 40). Pollen of *Luisia*, *Thrixspermum*, *Cleisostoma*, and *Haraella* have tectate-granular exines (Figs. 42, 44, 48, 50). The exine rests on a thin (*Thrixspermum*, Fig. 42) or thick (*Phalaenopsis*, Fig. 40; *Luisia*, Fig. 45; *Ascocentrum*, Fig. 47; *Cleisostoma*, Fig. 49) multilayered intine. Pollen interior in the pollinium are exineless and are surrounded by a thick, often elaborated intine (e.g., *Thrixspermum*) (Figs. 41, 43, 45, 47, 49, 51).

Vandeae–Zygopetalinae

Cochleanthes discolor (Lindl.) Schultes & Garay. Pollen grains occur in tightly packed pollinia. Pollen grains peripheral in the pollinium have a tectate-granular exine (Fig. 52), the granular layer resting directly on a bilayered intine (Fig. 52). Pollen grains interior in the pollinium lack exine and are surrounded only by the bilayered intine (Fig. 53).

Vandeae–Bifrenariinae

Rudolfiella aurantiaca (Lindl.) Hoehn. Pollen grains occur in tightly packed pollinia. Pollen peripheral in the pollinium have a tectate-granular exine, the granular layer resting directly on the intine (Fig. 54). The exine is perforated with minute channels (Fig. 54). Pollen in the interior of the pollinium are exineless, surrounded by a thin intine (Fig. 55); however, sporopolleninous granules occasionally are embedded in the thin intine.

Vandeae–Ornithocephalinae

Zygostates alleniana Kraenzl. Pollen grains occur in tightly packed pollinia. Pollen peripheral in the pollinium have a tectate-granular wall structure (Fig. 56); the granular layer rests directly on a

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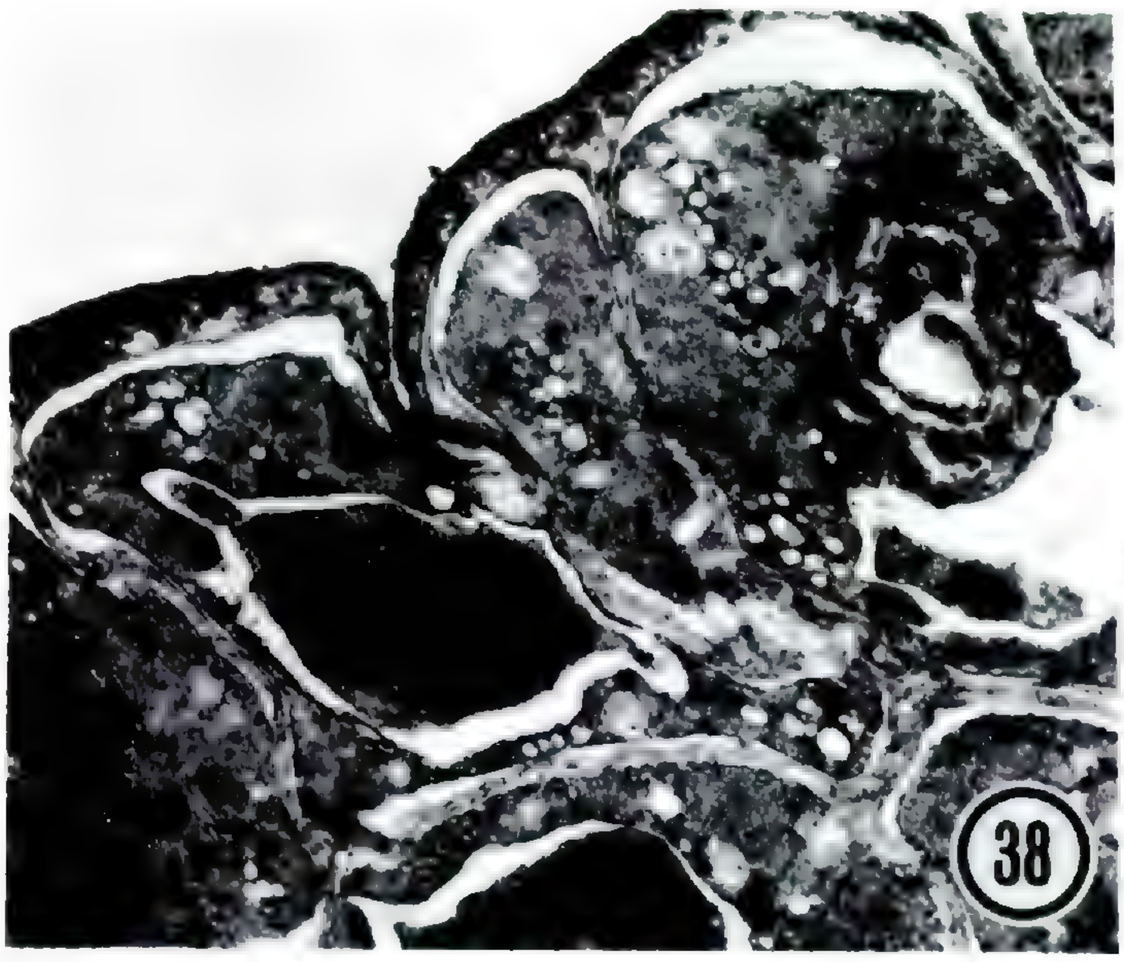
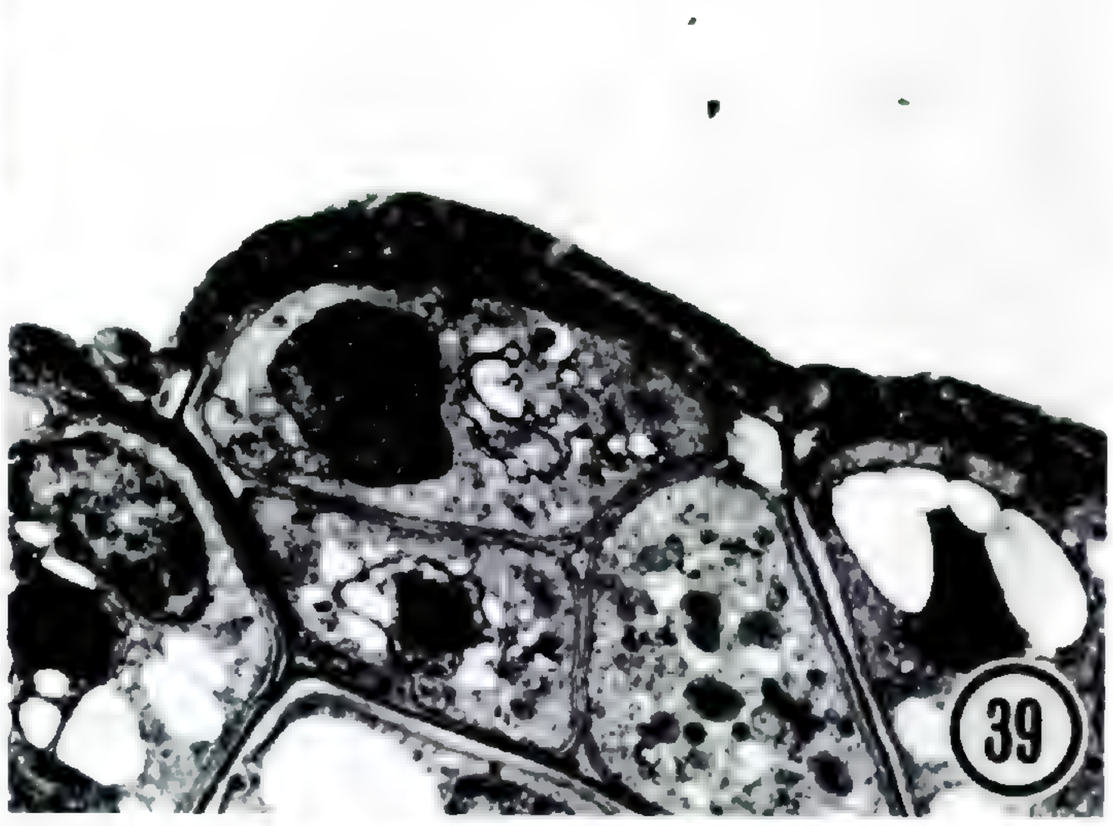
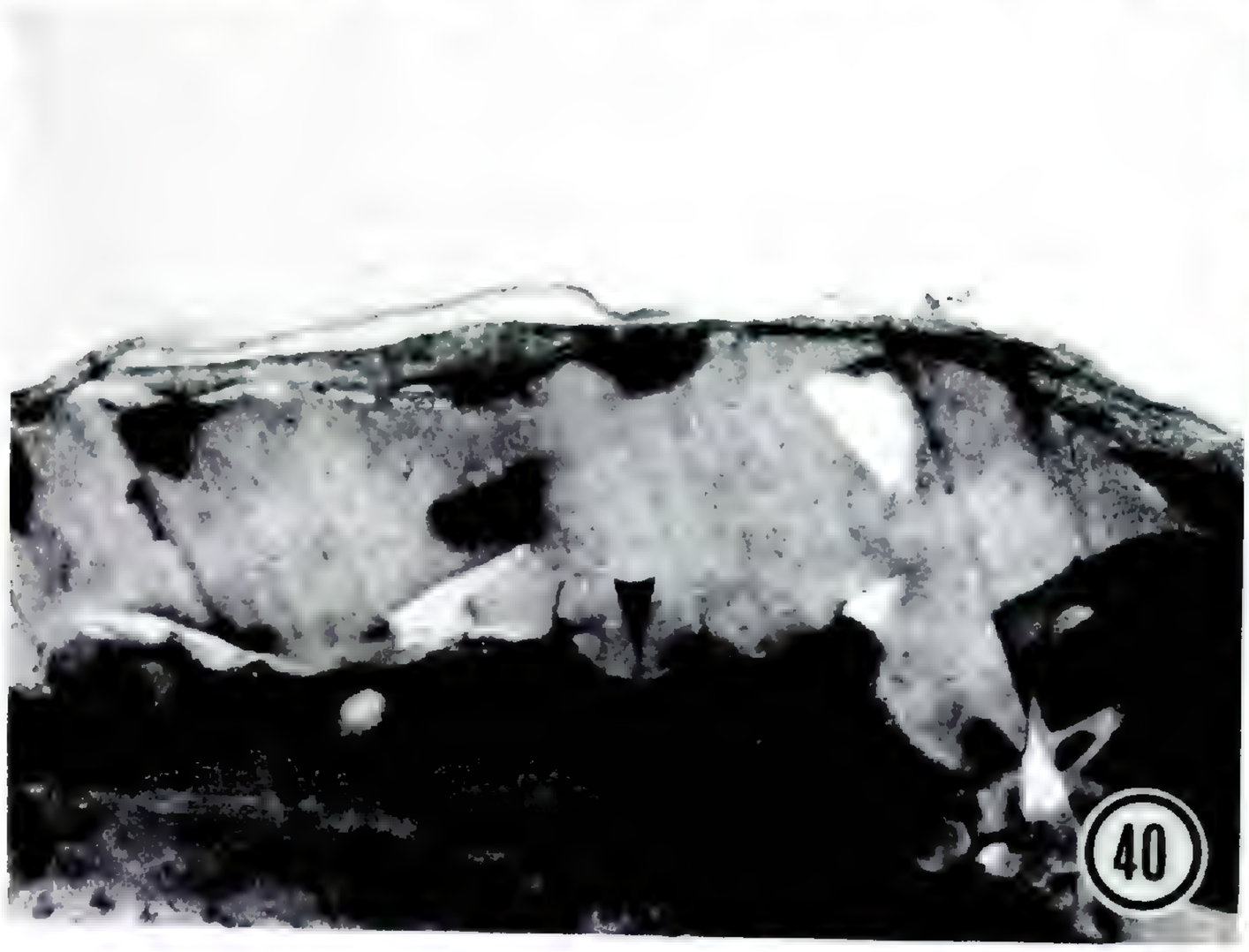
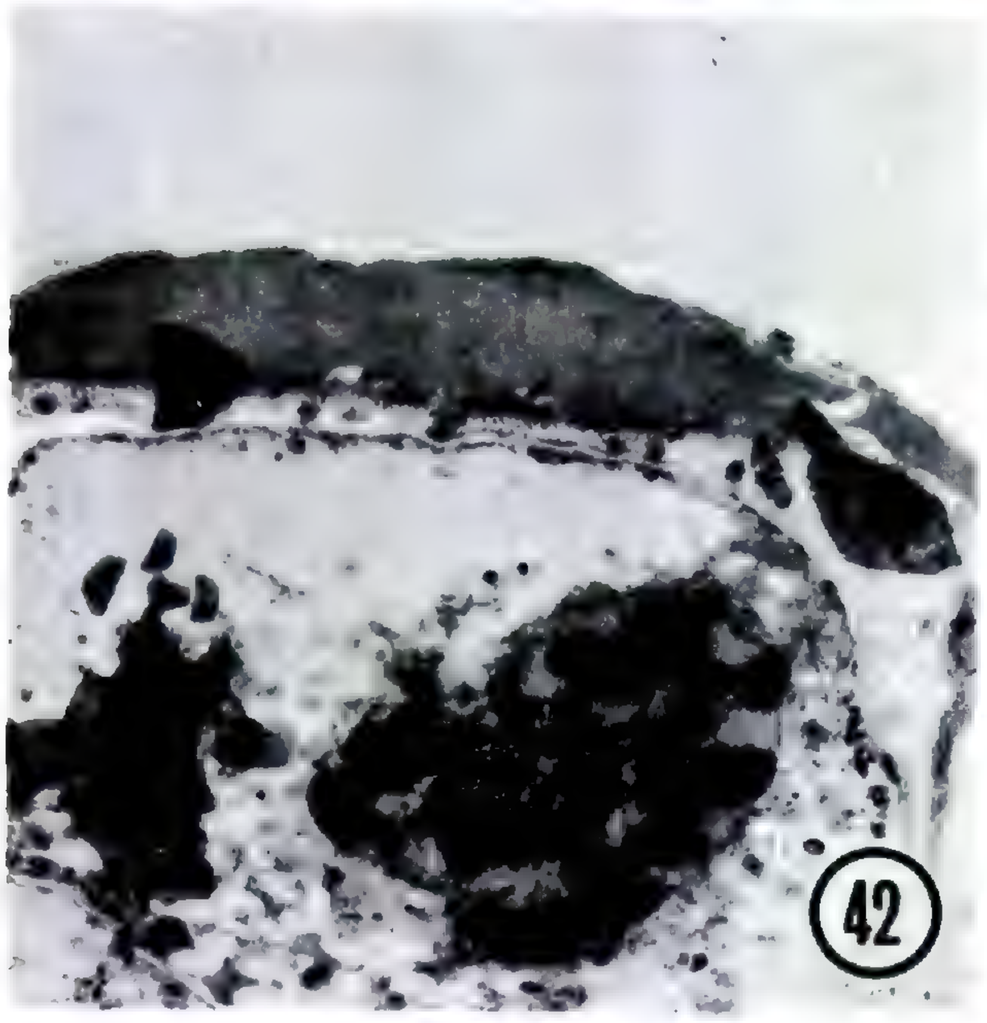
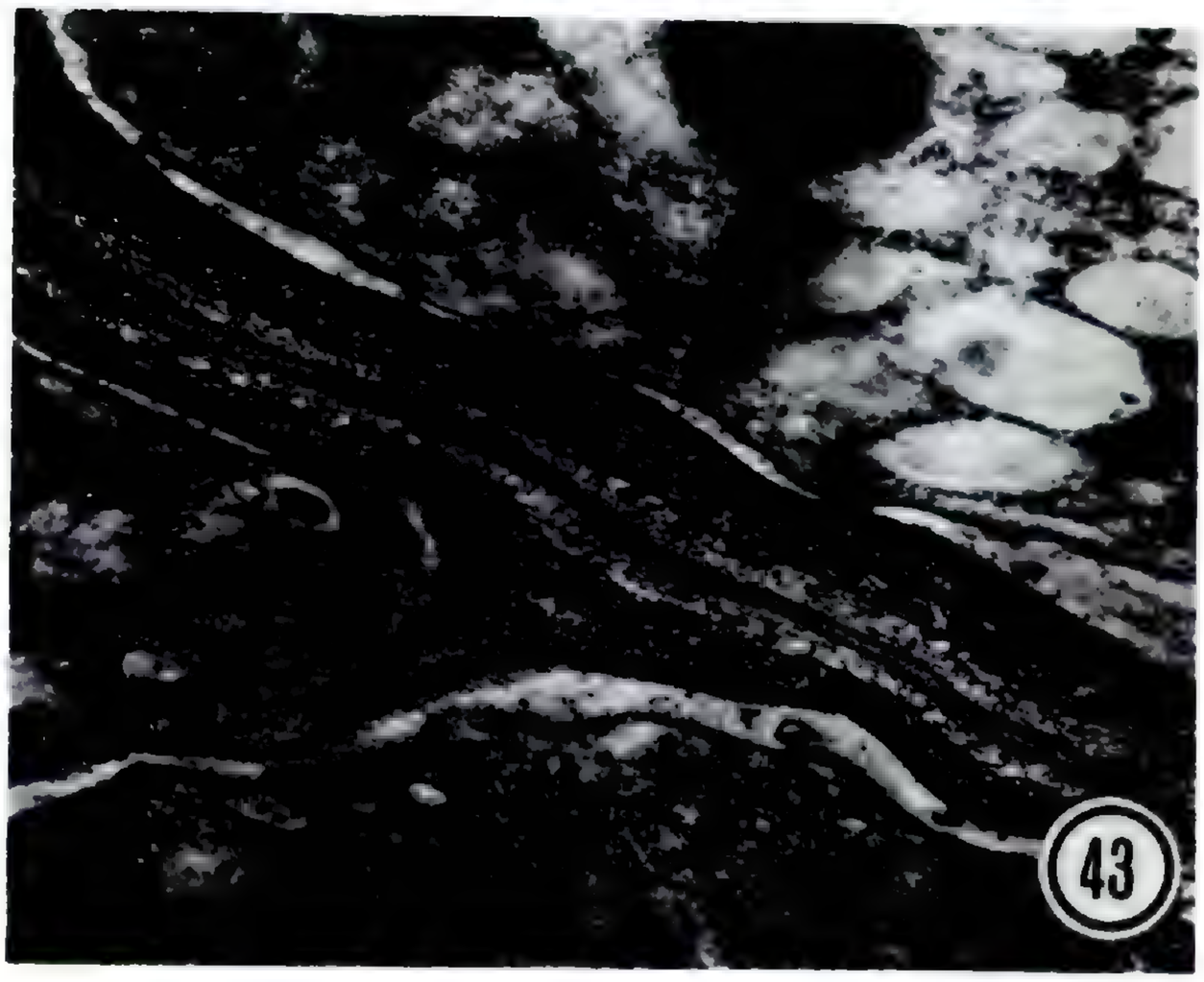
FIGURES 31–37. Pollen of the Epidendroideae.—31. Pollen peripheral in the pollinium of *Restrepia striata* showing atectate exine, ×20,500.—32. *R. striata* pollen showing sporopolleninous granules between adjacent pollen grains peripheral in the pollinium, ×16,000.—33. *R. striata* pollen interior in the pollinium showing the thin intine, ×10,000.—34. Pollen peripheral in the pollinium of *Dendrobium nobile* showing tectum and the dense granular layer that rests directly on a fibrillar intine, ×15,125.—35. Pollen interior in the pollinium of *D. nobile* showing bilayered intine, ×6,550.—36. Pollen peripheral in the pollinium of *D. aphyllum* showing the presence of only the fibrillar intine, ×5,300.—37. Pollen interior in the pollinium of *D. aphyllum* showing loosely packed pollen and the intine, ×3,450.



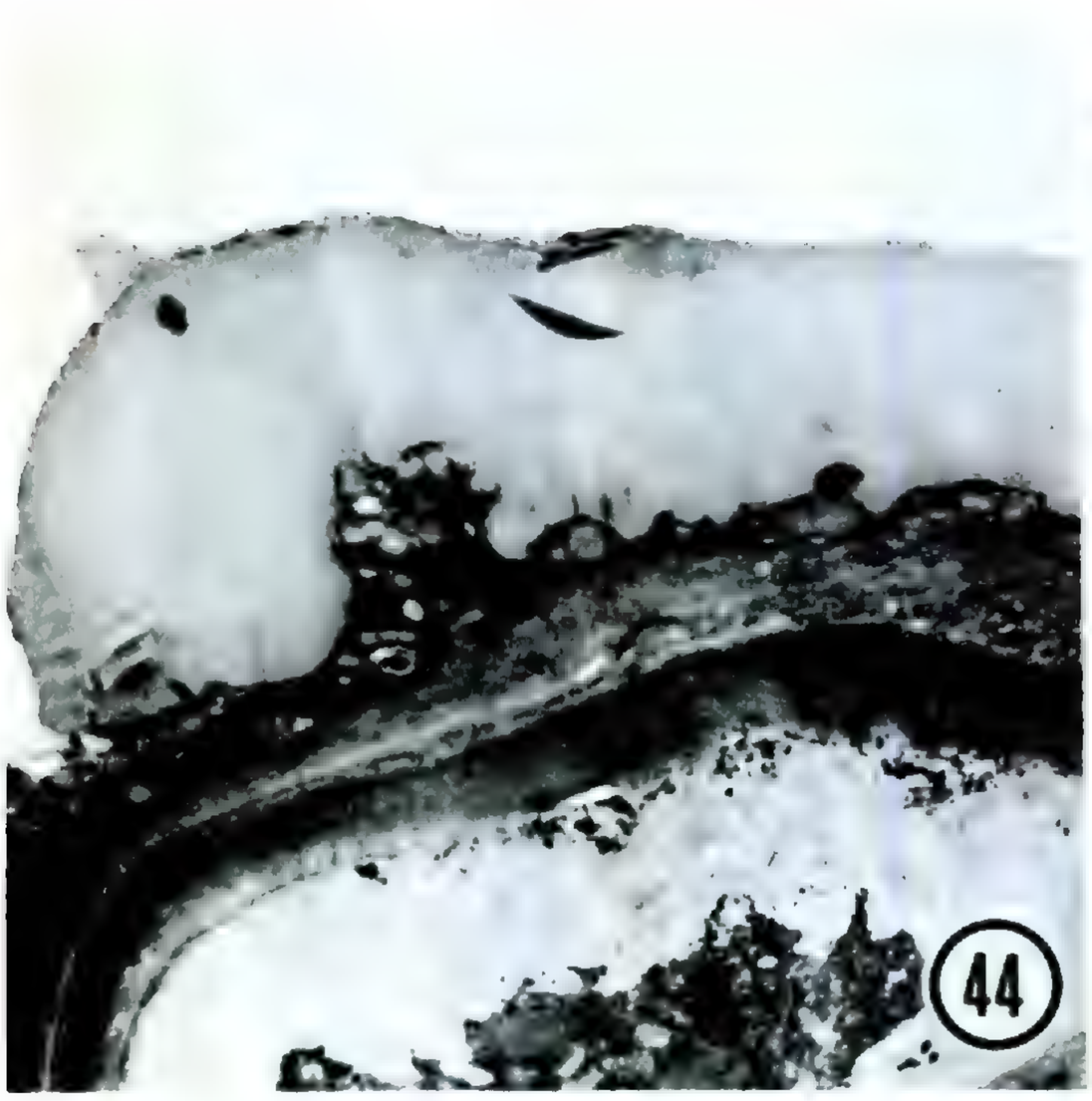


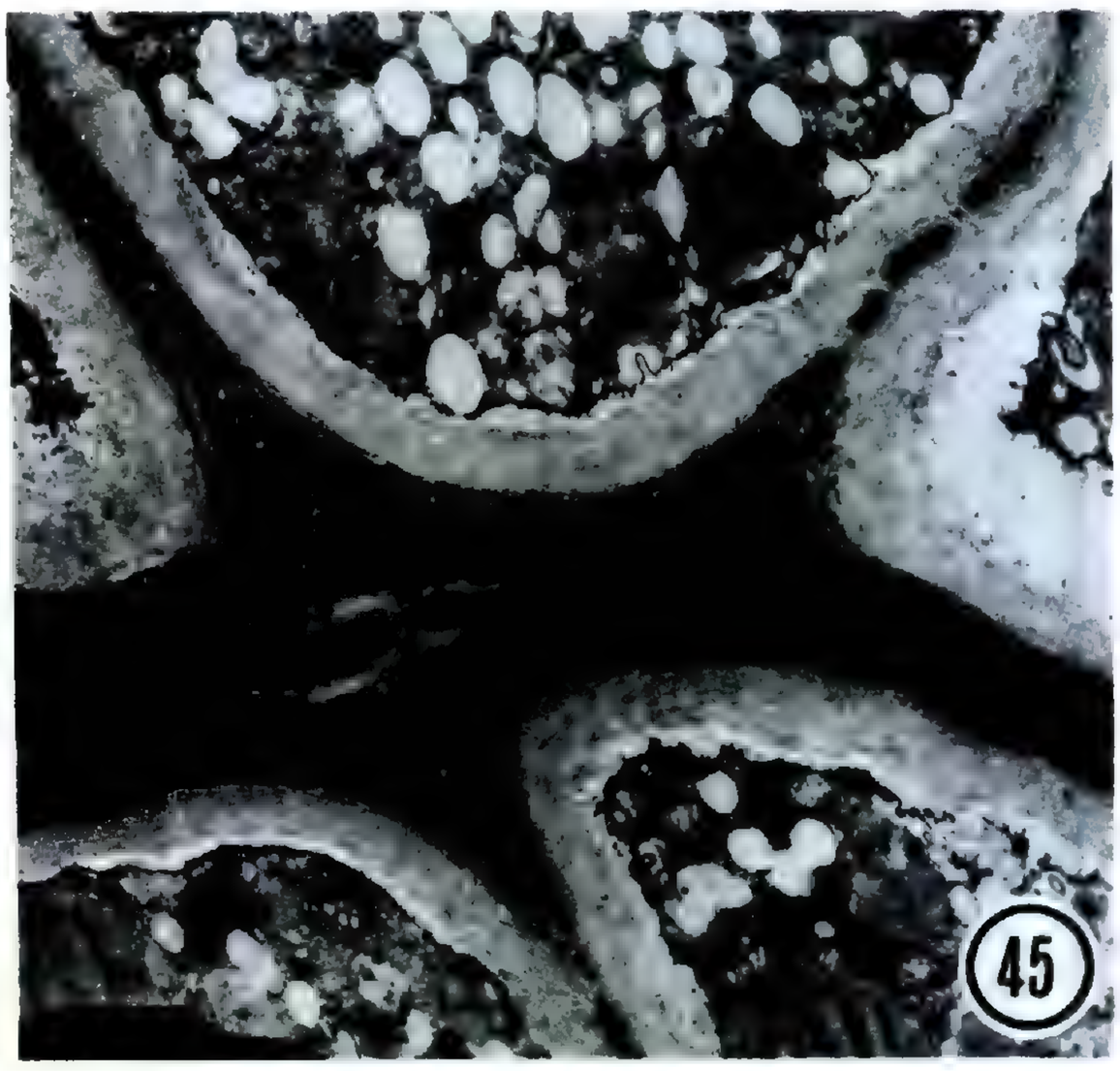


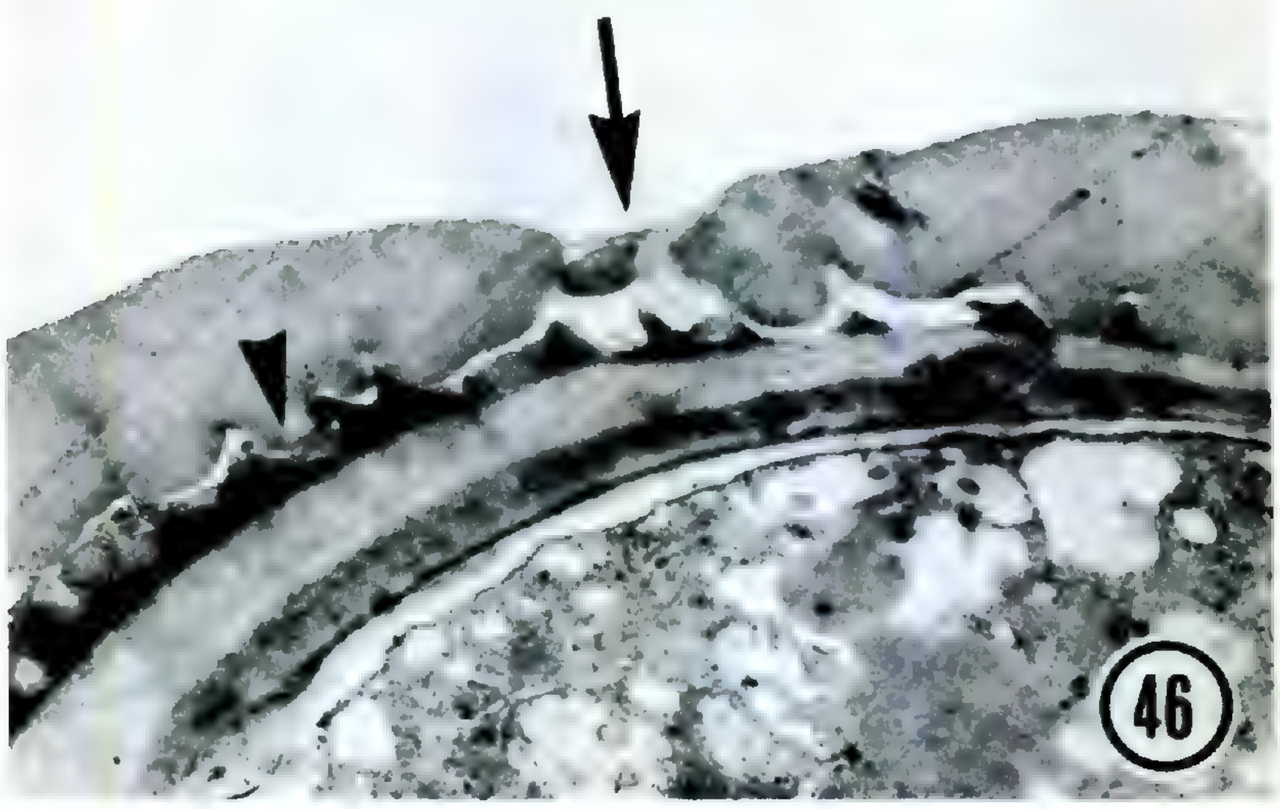


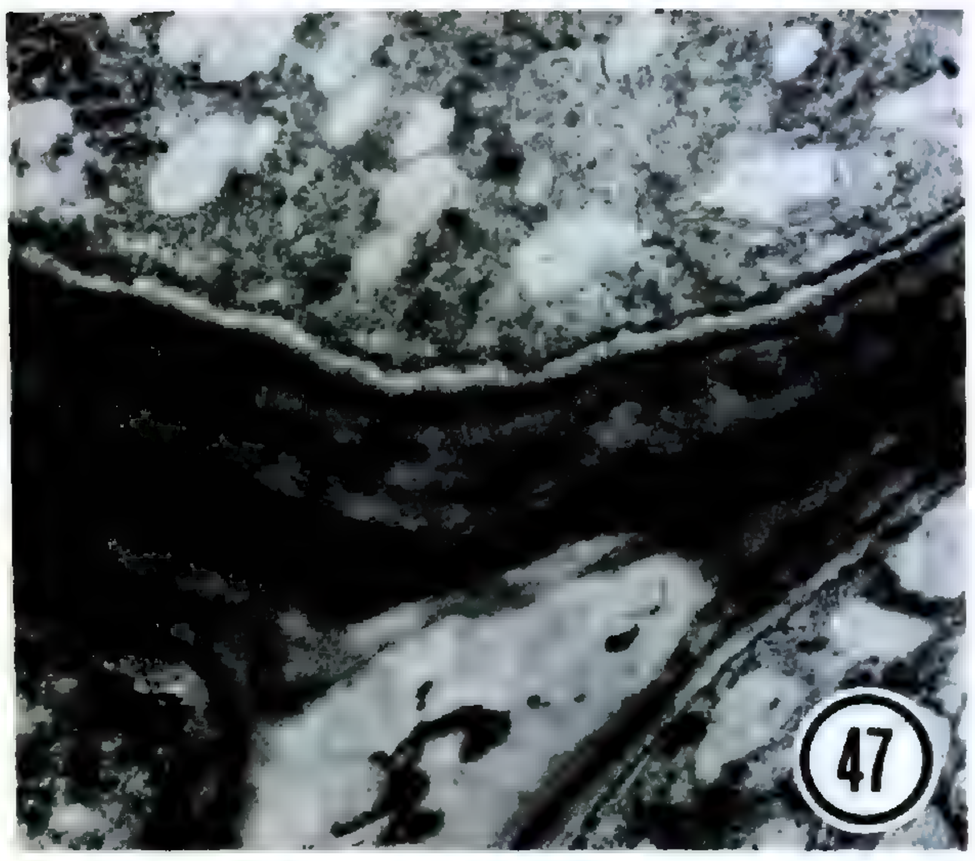


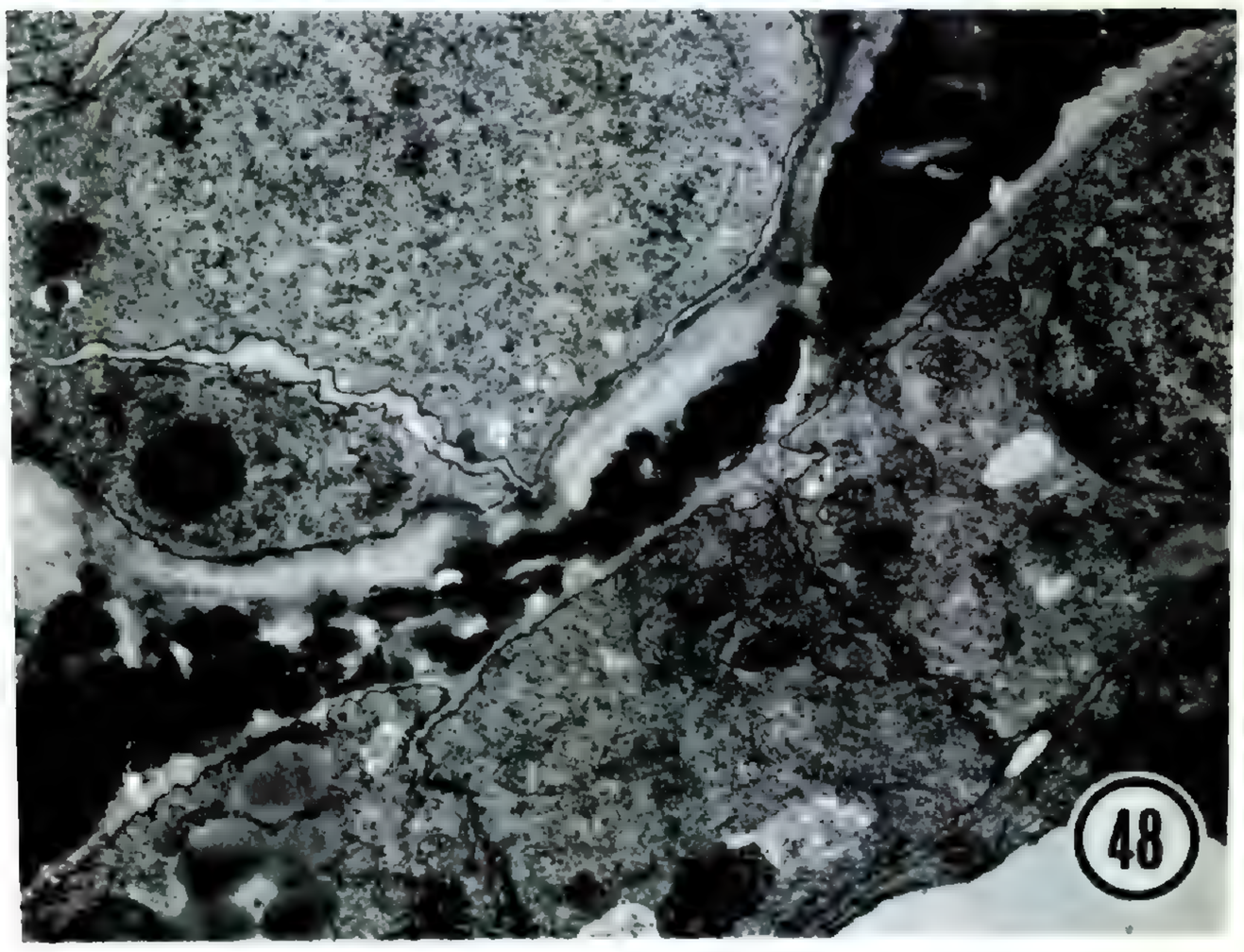
FIGURES 38–43. Pollen of the Epidendroideae.—38. Pollen of *Bulbophyllum imbricatum* showing outer grains with tectate-granular wall and exineless interior pollen grains, ×6,500.—39. Pollen of *Schoenorchis fragrans* showing the atectate exine that is continuous around the entire pollinium and exineless interior pollen grains, ×3,500.—40. Pollen peripheral in the pollinium of *Phalaenopsis lueddemanniana* showing atectate exine with endo-rugulations (arrowhead), ×20,500.—41. Exineless pollen interior in the pollinium of *P. lueddemanniana* showing multilayered intine, ×8,200.—42. Pollen peripheral in the pollinium of *Thrixspermum saruwatarii* showing the exine that is underlain by a scanty granular layer, ×6,500.—43. Exineless pollen interior in the pollinium of *T. saruwatarii* showing elaborated intine, ×28,500.

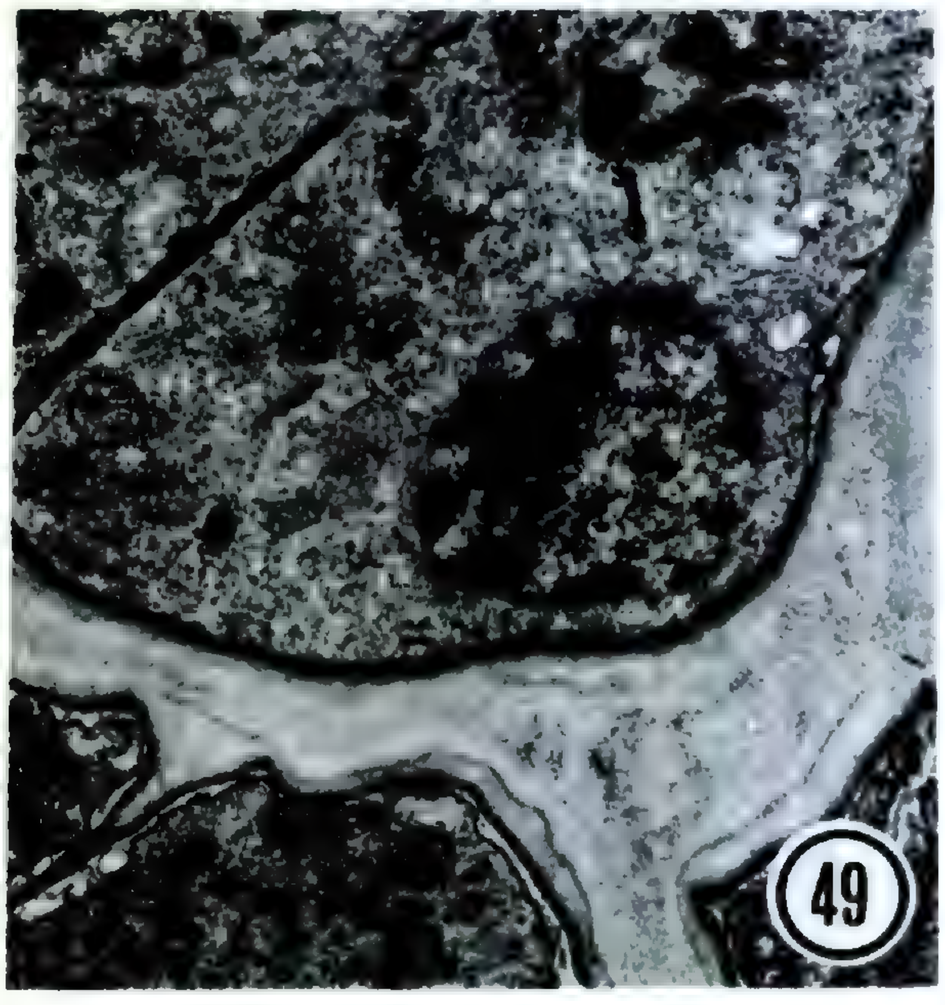




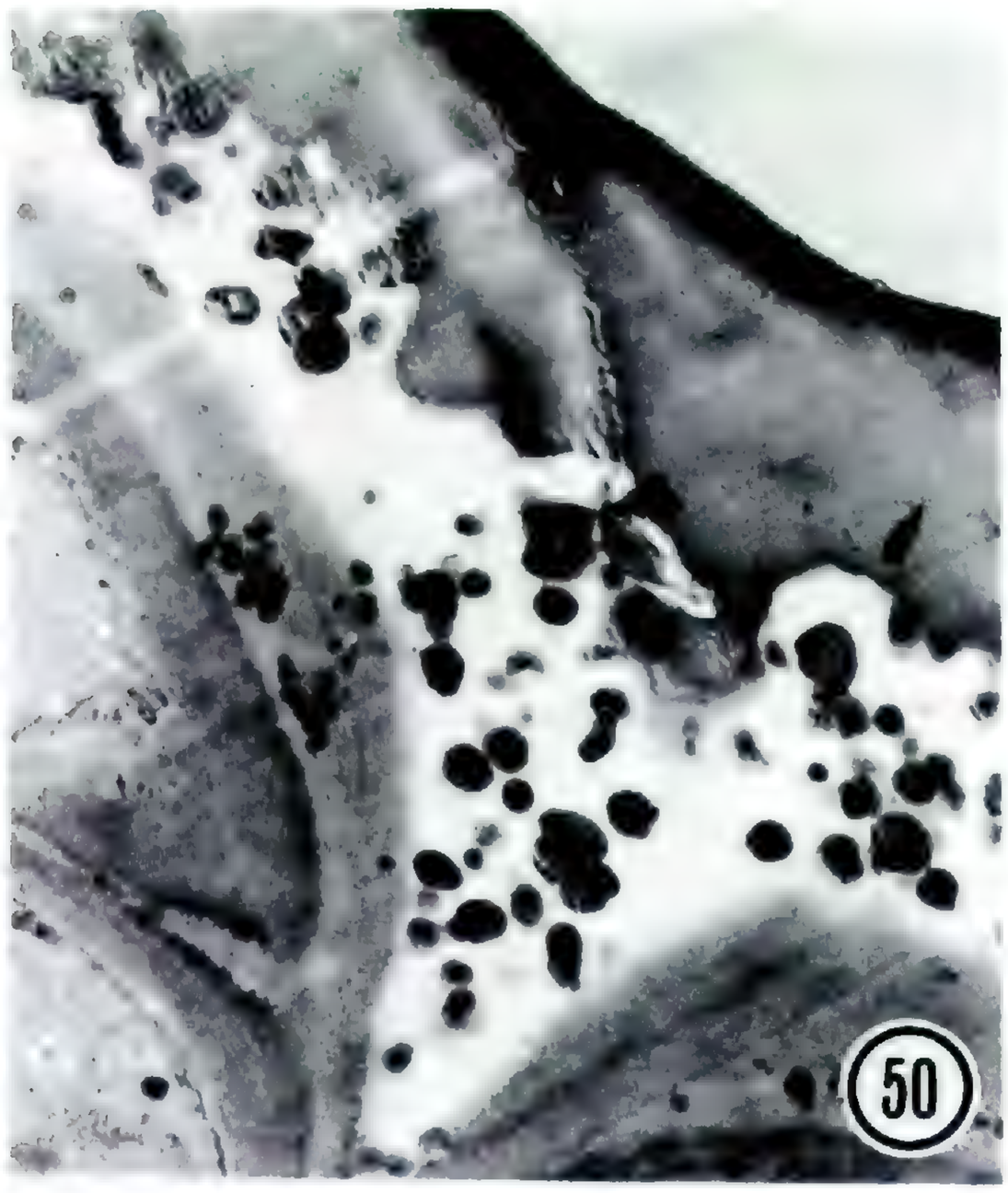








FIGURES 44–49. Pollen of the Epidendroideae.—44. Pollen peripheral in the pollinium of *Luisia teres* var. *botanensis* showing thick tectum and the thin granular infrastructural layer that rests directly on the bilayered intine, ×6,500.—45. Pollen interior in the pollinium of *L. teres* var. *botanensis* showing multilayered intine. Note the small granules embedded in the dense intinous layer (arrowhead), ×4,150.—46. Pollen peripheral in the pollinium of *Ascocentrum ampullaceum* showing atectate exine with endo-rugulations (arrowhead). Note the thinning of the exine; these thin areas may function as apertures (arrow), ×11,500.—47. Exineless pollen interior in the pollinium of *A. ampullaceum* showing multilayered intine, ×10,000.—48. Pollen of *Cleisostoma racemiferum* showing sporopollenous wall between adjacent pollen grains, ×7,100.—49. Exineless pollen inferior in the pollinium of *C. racemiferum*, ×3,500.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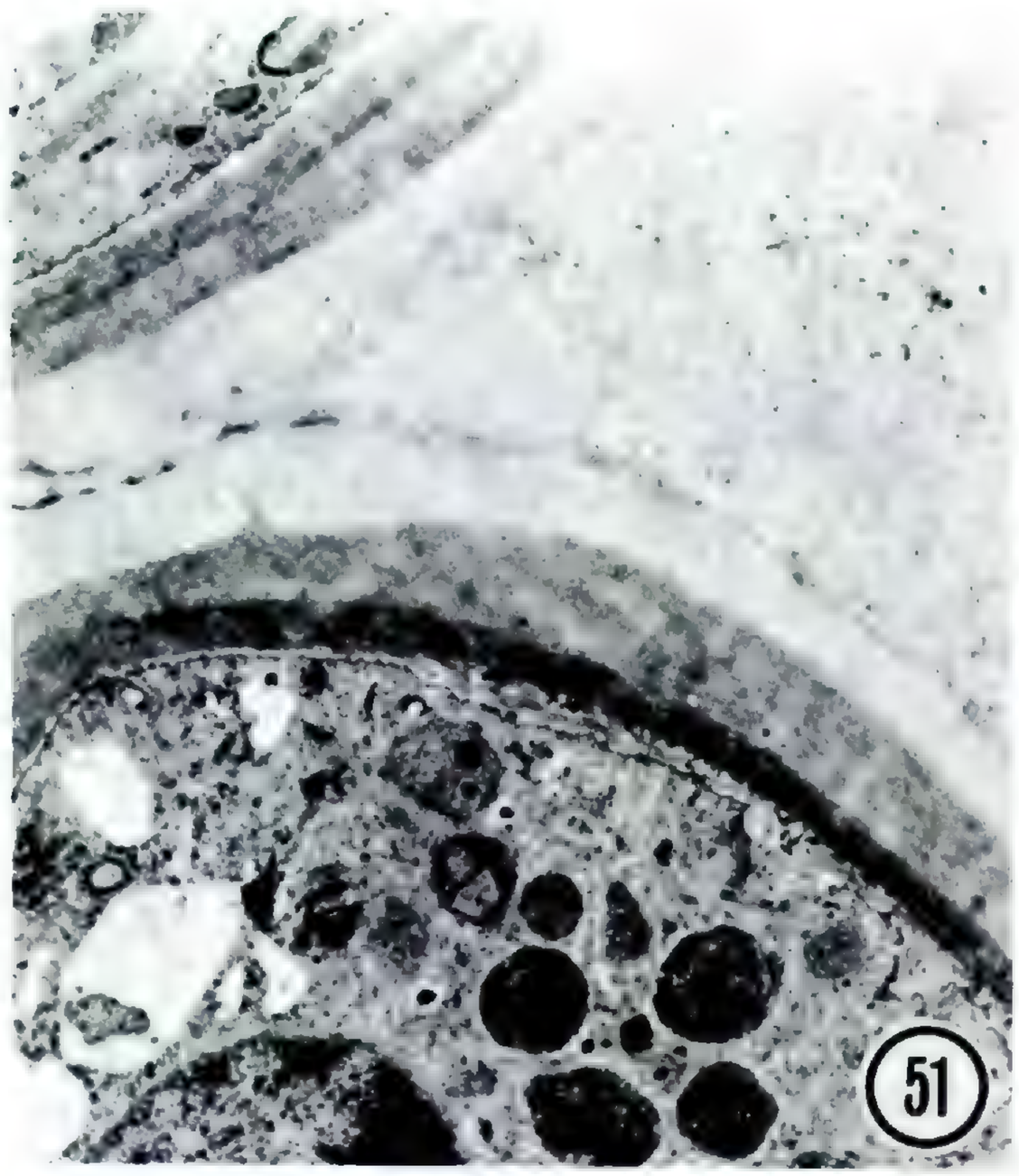
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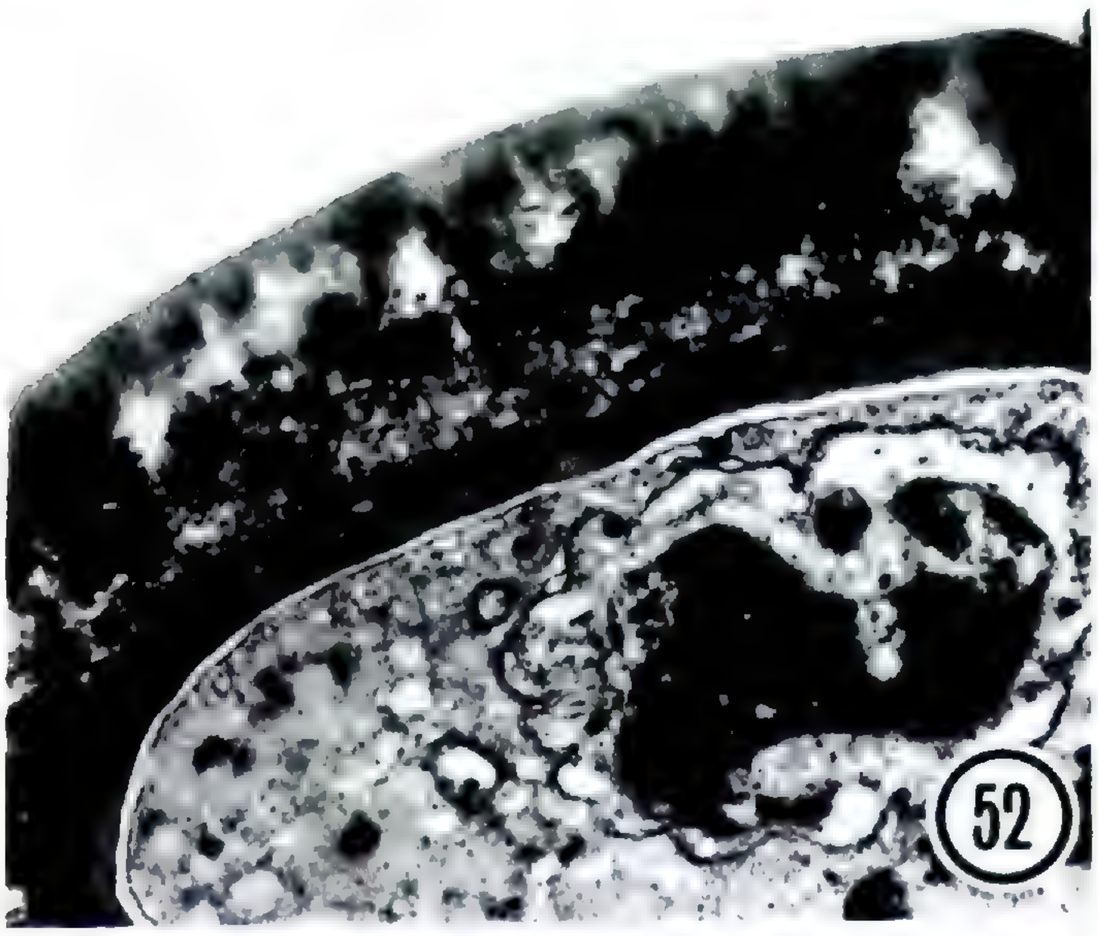
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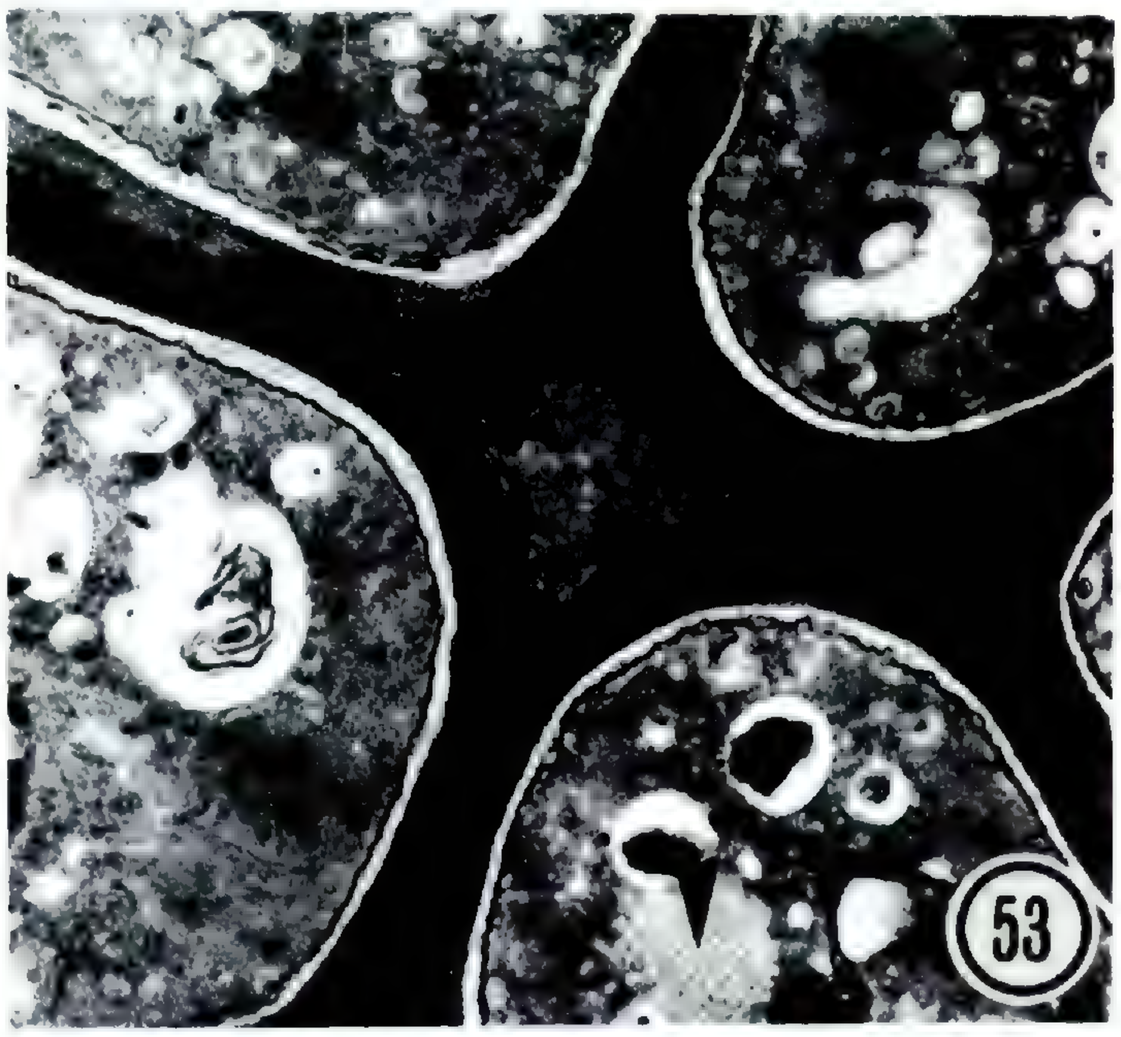
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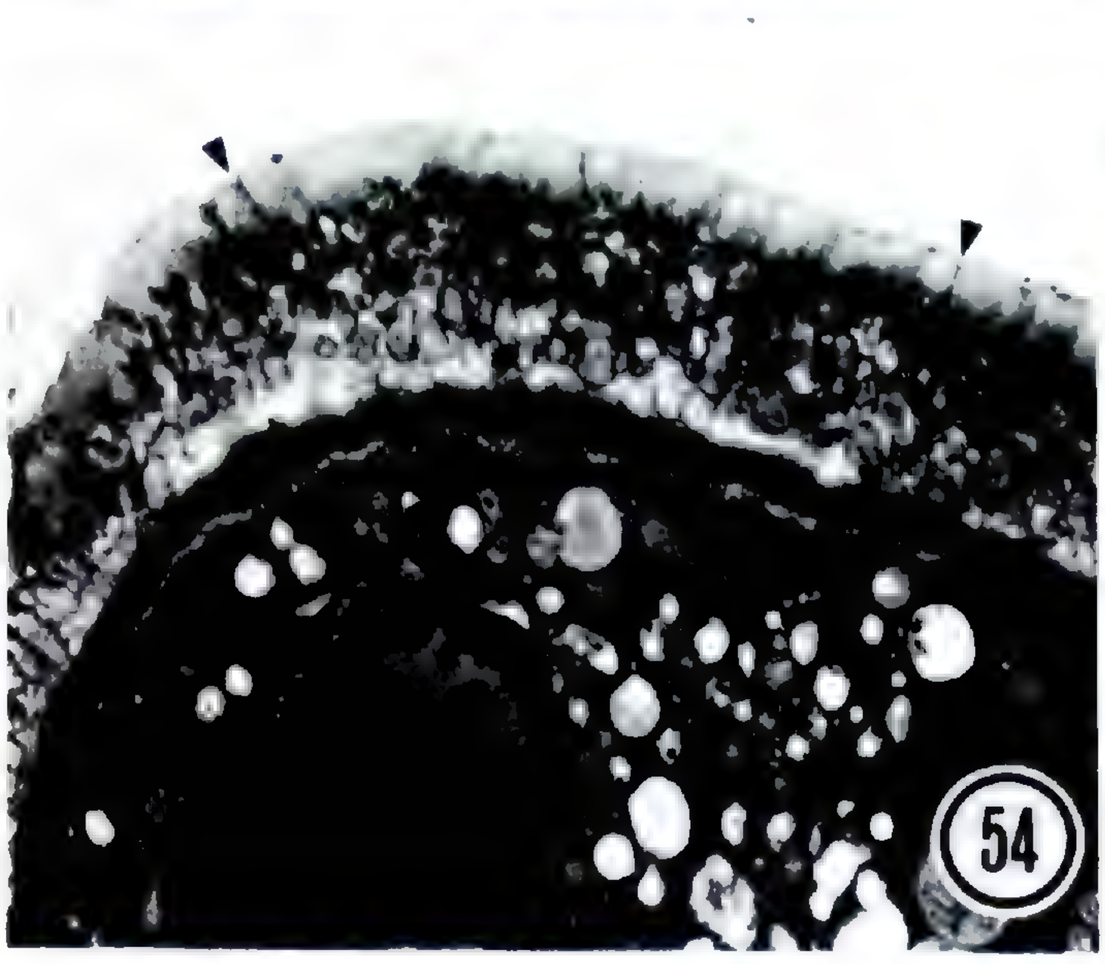
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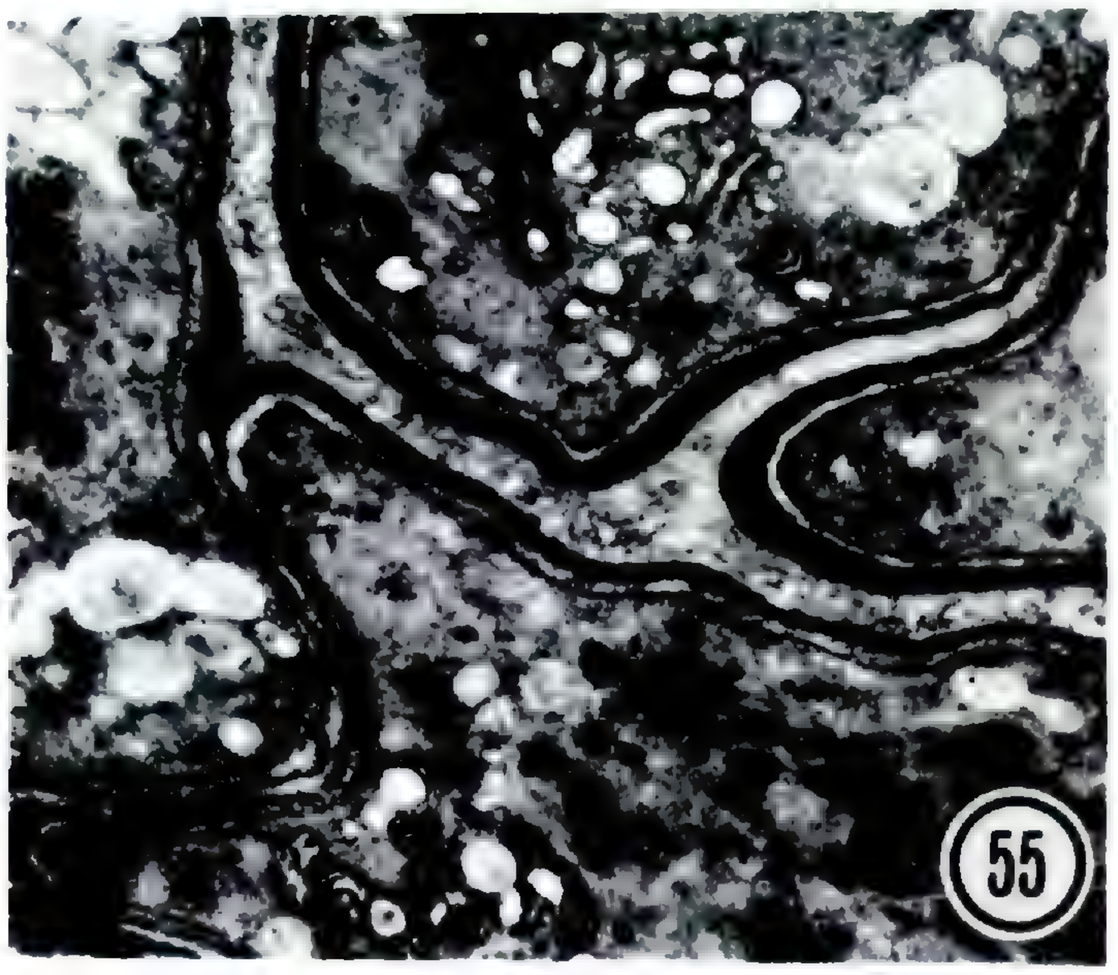
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bilayered intine (Fig. 56). In the tectum are urn-shaped structures of unknown function (this feature is not known to occur in any other pollen, gymnosperm, or angiosperm) (Fig. 56). Pollen grains in the interior of the pollinium are exineless and are surrounded by a bilayered intine (Fig. 57).

Cymbidieae

Cymbidium aloifolium (L.) Sw. Pollen grains occur in tightly packed pollinia. Pollen peripheral in the pollinium have a tectate-granular wall structure (Fig. 58), the granular layer resting directly on the intine (Fig. 58). The tectum is traversed by minute channels (Fig. 58). Pollen interior in the pollinium are loosely attached and exineless; the intine is the only wall layer present (Fig. 59). However, sporopolleninous granules are occasionally embedded in the intine (Fig. 59).

Cymbidieae–Oncidiinae

Trichophilia marginata Henfr. Pollen grains occur in tightly packed pollinia. Pollen peripheral in the pollinium have a tectate-granular wall structure (Fig. 60). The granular layer rests on a thin intine (Fig. 60). Pollen interior in the pollinium are exineless and surrounded by a multilayered intine (Fig. 61); however, sporopolleninous granules often occur in the contact areas between adjacent pollen grains (Fig. 61).

Discussion

Pollen grains from each of the five orchid subfamilies were studied ultrastructurally. Although the number of species studied is insubstantial in relation to the size of the family, the available data, when considered in the context of other morphological features, provide insight into the evolutionary trends of aperture and wall structure of the Orchidaceae.

Burns-Balogh (1983) has proposed evolutionary trends for exine structure of orchid pollen. She considered pollen of the Apostasioideae most primitive. This is based on the pollen characters associated with unspecialized reproductive organs of the subfamily. The pollen wall of *Apostasia* is tectate-perforate-columellate with a well-developed footlayer. Burns-Balogh (1983) recognized two major lines diverging from the Apostasioideae. One line culminates in the tectate-imperforate-granular wall of the Cypripedioideae via a tectate-imperforate-columellate wall. The other line progresses to the tectate-perforate-columellate type, eventually giving rise to tectate-granular wall types of the Orchidoideae and Epidendroideae with the loss of the footlayer. In all of these types Burns-Balogh (1983) recognized the common occurrence of endexine. Endexine does not usually occur in monocots (Zavada, 1983), and this wall layer has not been unequivocally demonstrated in orchids: the footlayer or infrastructural layer in all cases rests directly on a fibrillar intine. Although Burns-Balogh's (1983) treatment of evolutionary trends of wall structure in orchids may be reasonable, the small sample size does not permit placing the large subfamilies in an evolutionary sequence based on pollen alone. In addition, some workers have suggested that the large subfamily Epidendroideae may be polyphyletic (Dressler, 1983). The data in the present contribution will be treated in terms of major evolutionary trends of pollen wall structure within the Orchidaceae (not necessarily representing cladistic relationships). This will be subject to revision and refinement as data accumulate on pollen ultrastructure in this family.

Three major trends are evident in the Orchidaceae. The first and most obvious is toward adherence of pollen grains into polyads (pollinia). This trend is best developed in the Orchidaceae and does not characterize many other monocot groups. However, polyads occur in the dicots (e.g., Asclepiadaceae, Fabaceae). In dicots with polyads, there is observed a pollen wall ultrastructure comparable to that of the orchids, i.e., a shift from the tectate-columellate wall structure in the taxa considered least specialized to tectate-granular or atectate in the taxa considered derived (Dicko-Zafimahova &

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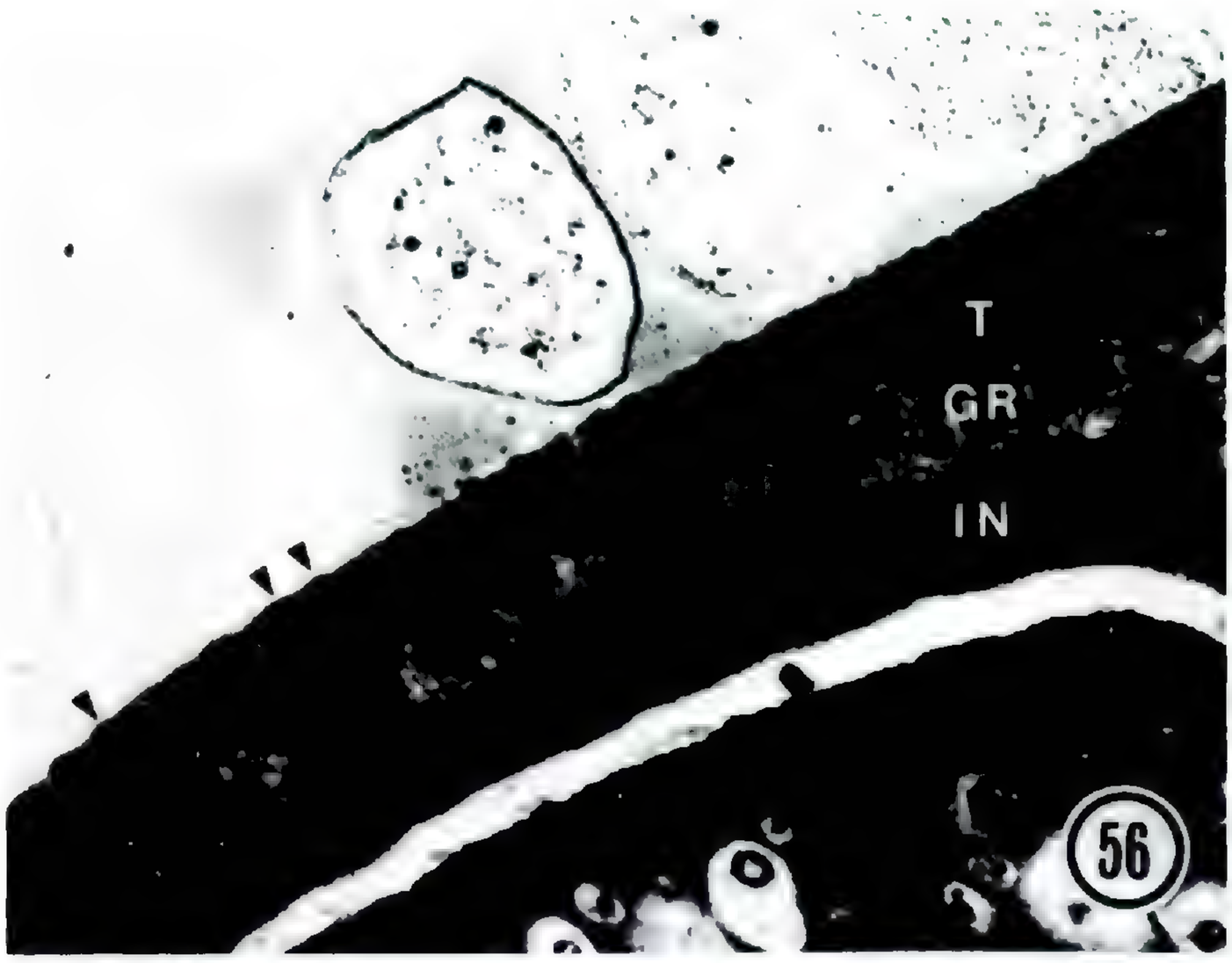
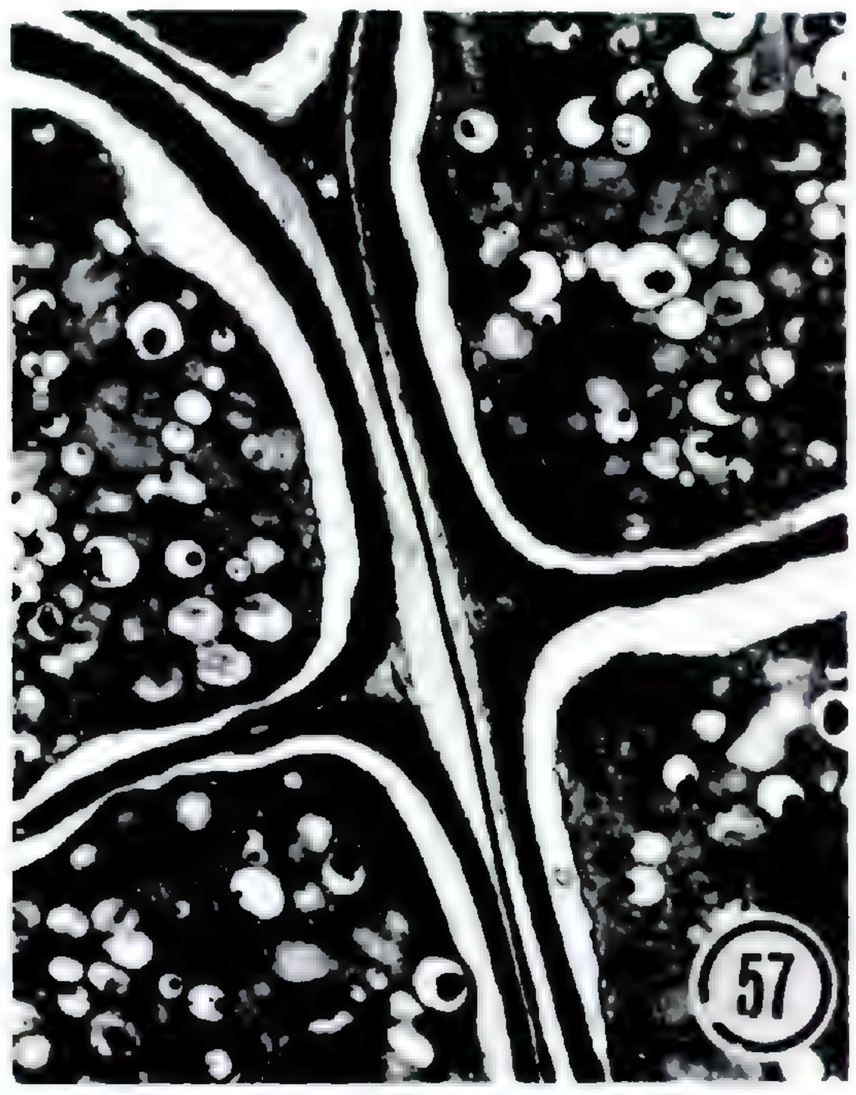
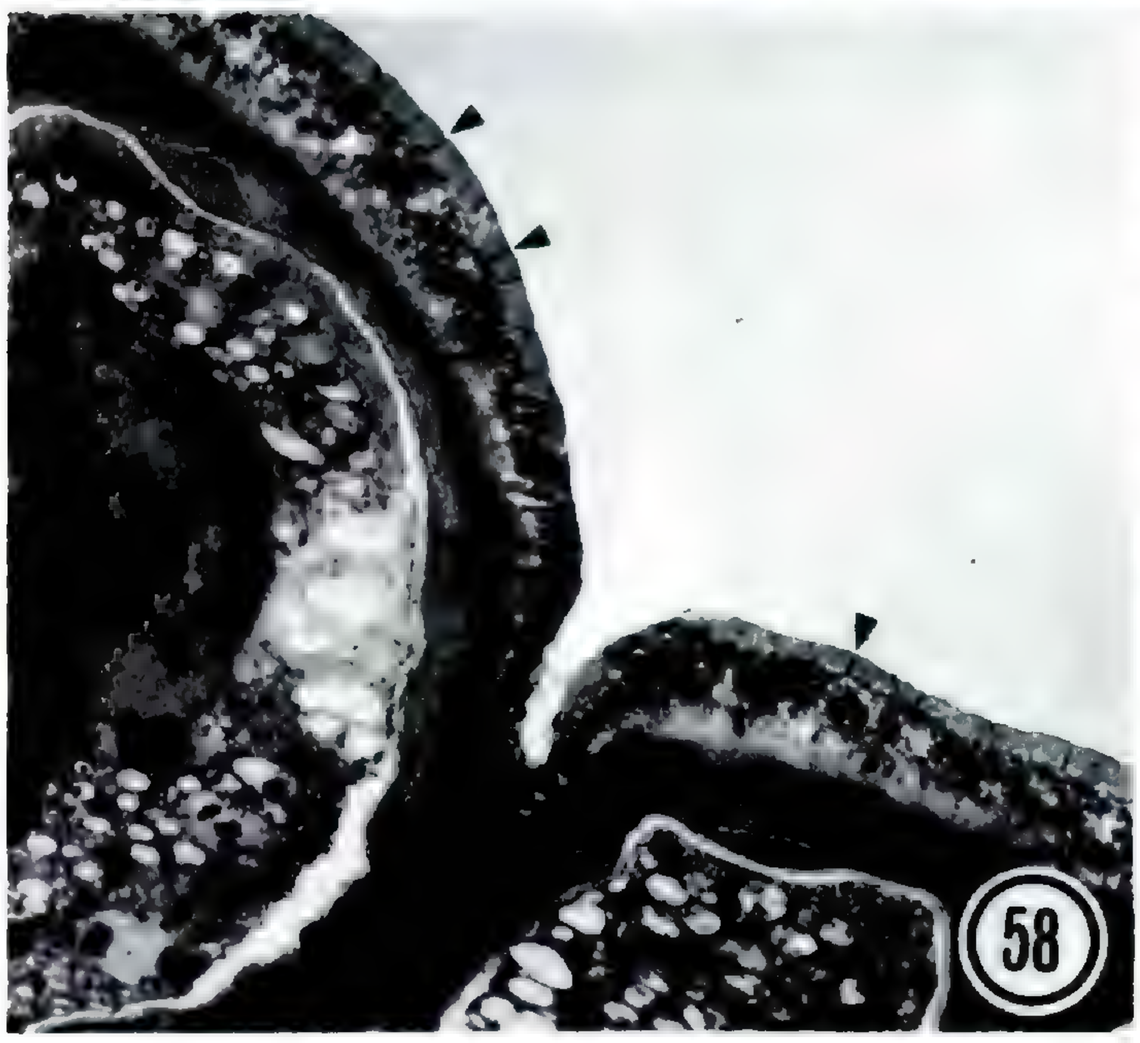
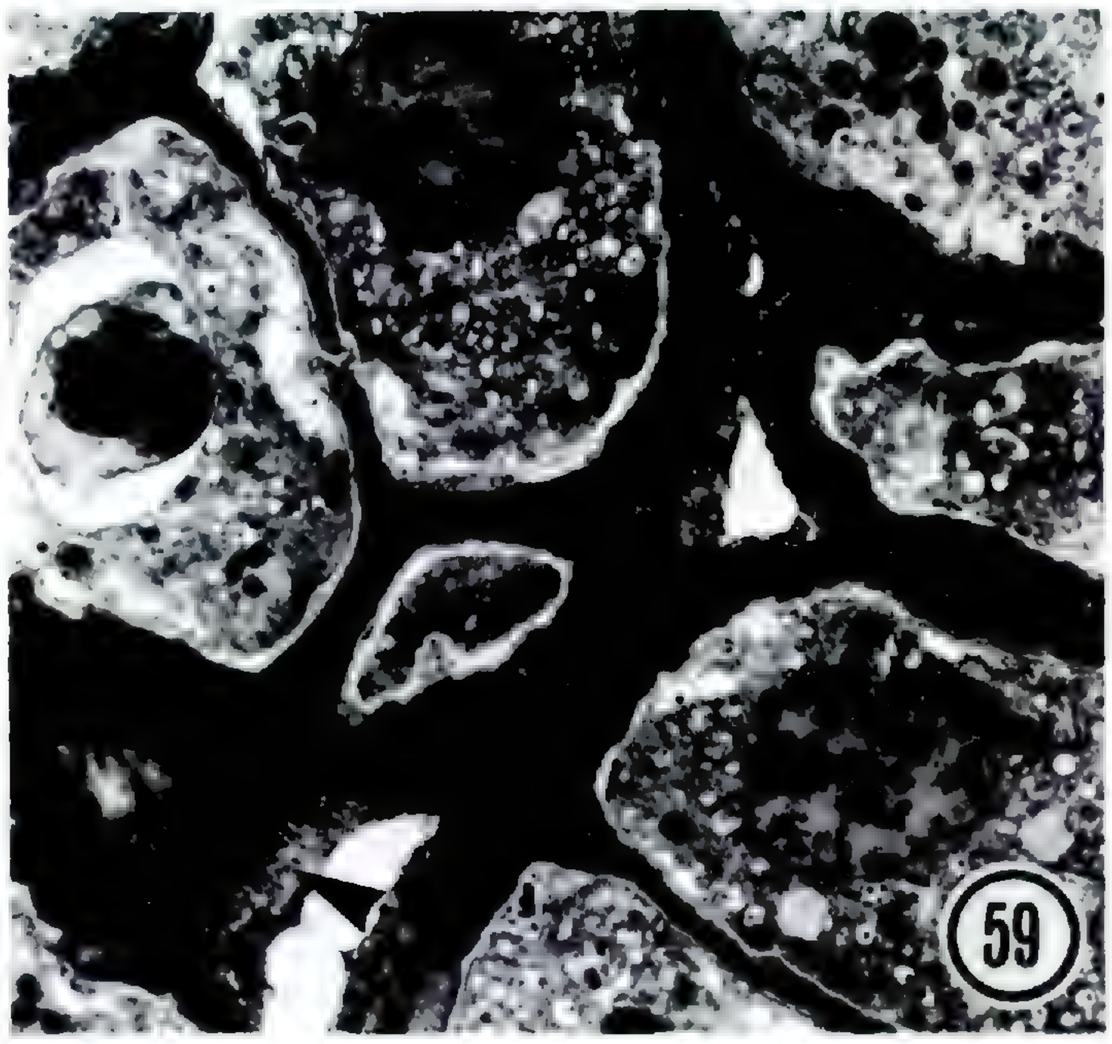
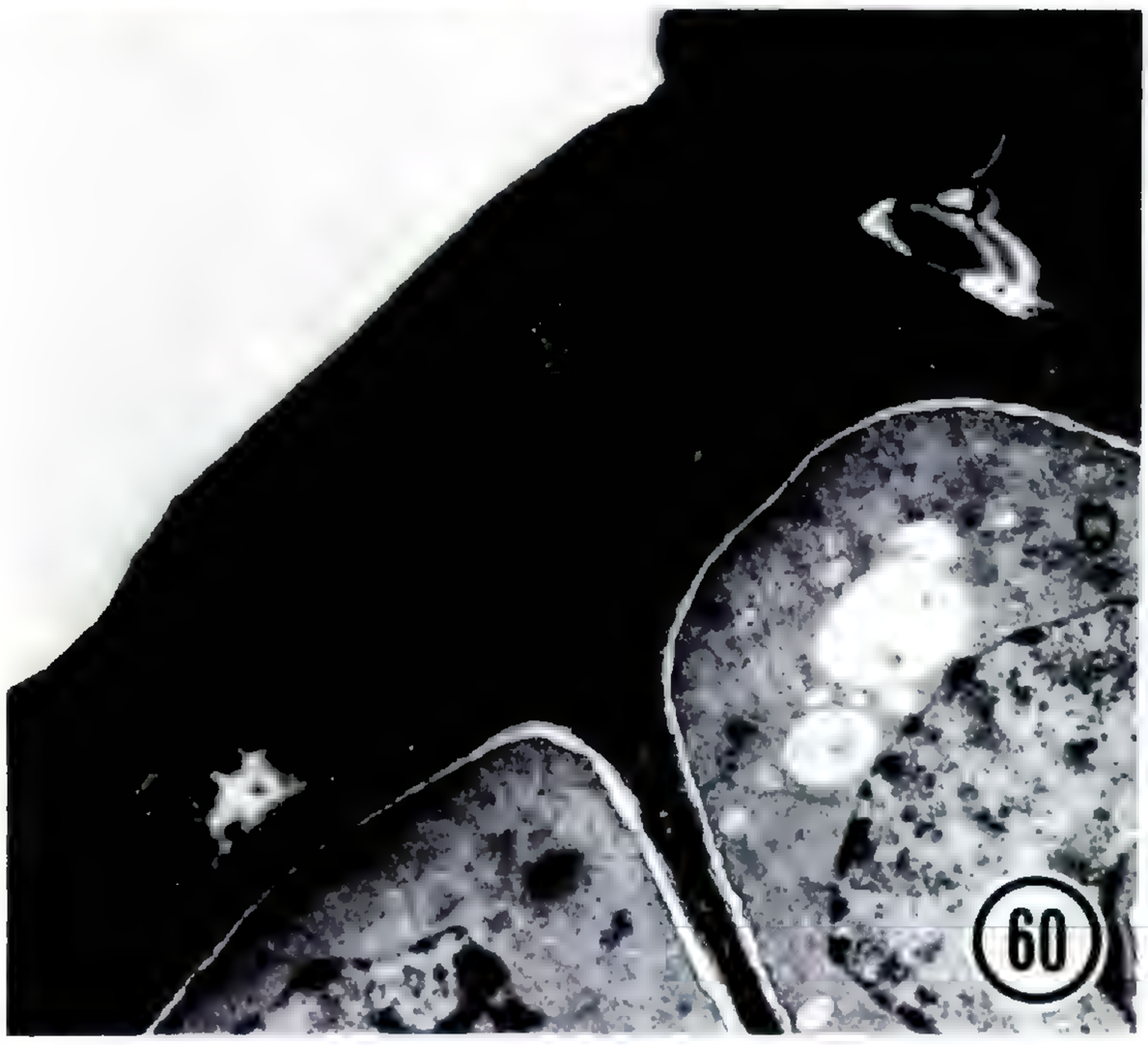
Figures 50–55. Pollen of the Epidendroideae.—50. Pollen peripheral in the pollinium of *Haraella retrocalla* showing the thick continuous tectum and scanty granular infrastructure, ×7,850.—51. Exineless pollen interior in the pollinium of *H. retrocalla* showing bilayered intine, ×7,850.—52. Peripheral pollen in the pollinium of *Cochleanthes discolor* showing tectum, granular infrastructure, and bilayered intine, ×10,000.—53. Exineless pollen interior in the pollinium of *C. discolor* showing intine. Note paracrystalline material of unknown composition (arrowhead), ×10,000.—54. Pollen peripheral in the pollinium of *Rudolfiella aurantiaca* showing tectum (with microchannels, arrowheads), granular infrastructure, and thin intine, ×10,000.—55. Exineless pollen interior in the pollinium of *R. aurantiaca* showing bilayered intine, ×10,000.

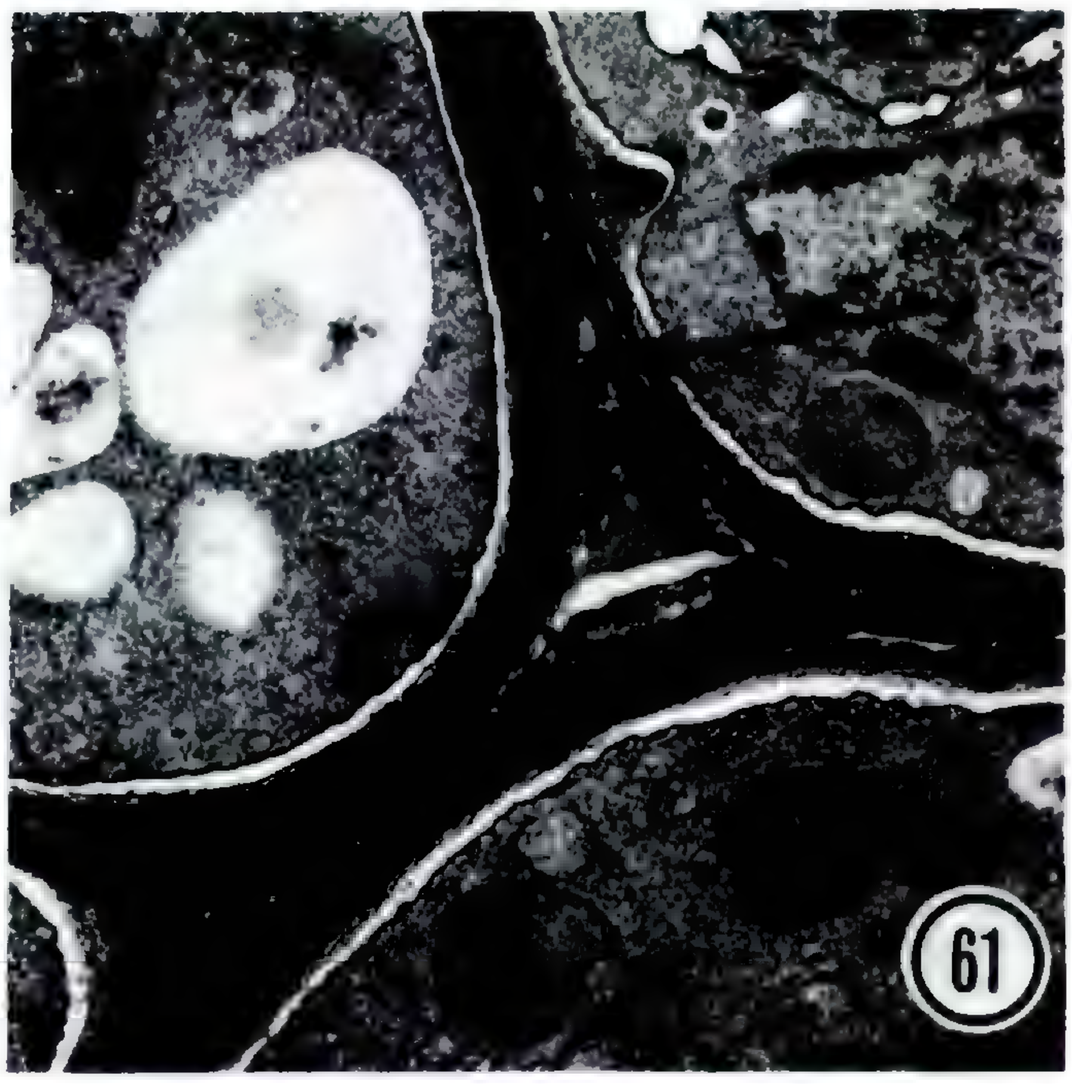












FIGURES 56–61. Pollen of the Epidendroideae. —56. Pollen peripheral in the pollinium of *Zygostates alleniana* showing tectum (T) with the unusual urn-shaped structures of unknown function (arrowheads), granular infrastructure (GR), and intine (IN), ×11,500.—57. Exineless pollen interior in the pollinium of *Z. alleniana* showing intine,

Audran, 1981). This raises the possibility that pollen wall structure in taxa with polyads may be more related to the spatial configuration of the pollen and development of the sporopolleninous wall around the pollinia than a reflection of the evolutionary level attained by a particular taxon.

Within the Orchidaceae the Apostasioideae have monads, but polyads and/or mealy pollinia occur in the Cypripedioideae and Spiranthoideae. The Orchidoideae and Epidendroideae have tightly packed, waxy pollinia (Dressler, 1981, 1983).

The second trend is toward a well-defined sulcus in the Apostasioideae, an ill-defined ulcerate pore in some Cypripedioideae and Spiranthoideae, and the inaperturate condition in the Orchidoideae and Epidendroideae (Zavada, 1983). The monosulcate condition is found in the least specialized subfamily, Apostasioideae. In the more derived subfamilies (Cypripedioideae, Spiranthoideae) the ulcerate condition is known, and in the most derived taxa (Epidendroideae) the inaperturate condition is prevalent. These trends in apertures parallel those observed in the other monocot groups, and in general, are characteristic of pollen of the Alismatideae and Zingiberidae (monosulcate to inaperturate condition). The Commelinideae exhibit a parallel trend in the reduction of the sulcus to an ill-defined pore, but here culminate in the development of a well-defined graminoid pore. The inaperturate condition is not observed in this group (Zavada, 1983).

The third major trend concerns exine structure and stratification. The occurrence of the tectate-columellate wall structure and monosulcate aperture in the Apostasioideae is typical of numerous monocot families including those generally considered primitive (Zavada, 1983 and references therein). There are a number of species in the more derived subfamilies that exhibit primitive wall structure type (tectate-columellate; Cypripedioideae, Spiranthoideae, Orchidoideae, and a few Epidendroideae). However, the primitive wall structure type often occurs with the more derived apertural types and pollen units. The combination of primitive and derived features in the few taxa investigated does not reveal the phylogenetic relationships among the Apostasioideae and these other subfamilies. In addition, the derived wall structure types (tectate-granular) also occur in the derived taxa (e.g., Orchidoideae and Epidendroideae).

The Vandeae consistently exhibit the tectate-granular and atectate wall types, no footlayer, inaperturate pollen, and compact pollinia, suggesting this is the most palynologically derived group of the family.

The orchids parallel many of the palynological evolutionary trends proposed for the other monocots (Zavada, 1983). However, a few features are unique to the monocots and the Orchidaceae in general. The first is loss of the sulcus via the ulcerate-porate condition. This is a major monocot trend, but is relatively rare in dicots. This trend, as mentioned above, occurs in the Alismatideae, Zingiberidae, and in part, the Commelinideae. The second is the occurrence of the tectate-columellate wall structure in monocots considered primitive and the least specialized orchid subfamily, Apostasioideae. The more advanced taxa have the tectate-granular, atectate, or exineless pollen. This is also a major monocot trend and is restricted to only a few dicot groups. Although some derived dicots have a granular or atectate wall structure, these wall structure types are thought to be primitive in some dicots (Walker, 1974). Concomitant with the loss of the tectum, infrastructure, and footlayer, there is elaboration of the intine in many monocots including the Orchidaceae. The occurrence of the elaborated intine is often found in monocot taxa that have specialized pollination mechanisms (e.g., Cannaceae, Kress & Stone, 1982). However, the morphological diversity and significance of the intine to pollination mechanisms and reproductive biology need to be investigated further.

Further pollen studies of orchids will undoubtedly bring many surprises. It is significant that orchids exhibit a wide range of pollen types that occur in the most primitive to the most derived monocots. Further detailed palynological studies of orchids and closely related families will be important to our understanding of pollen evolution, not only in the Orchidaceae, but in the monocots in general.

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×5,300.—58. Peripheral pollen in the pollinium of *Cymbidium aloifolium* showing microchannelled tectum (arrowheads), granular infrastructure, and thick intine, ×5,300.—59. Pollen interior in the pollinium of *C. aloifolium* showing intine with minute sporopolleninous granules (arrowhead), ×3,450.—60. Pollen peripheral in the pollinium of *Trichophila marginata* showing thick tectum and massive granular infrastructure that rests on a thin intine, ×6,500.—61. Pollen interior in the pollinium of *T. marginata* showing sporopolleninous granular layer (arrow) and dense intine, ×11,500.

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APPENDIX I. Specimens investigated in this study.

Acanthephippium sylhetense Lindl., Christenson 381 CONN, India

Ascocentrum ampullaceum (Roxb.) Schltr., Christenson 404 CONN, Thailand

Bletilla striata (Thunb.) Reichb. f., Christenson 374 CONN, Japan

Bulbophyllum imbricatum Lindl., Christenson 426 CONN, Africa

Cattleya skinneri Batem., Christenson 393 CONN, Costa Rica

Cleisostoma racemiferum (Lindl.) Garay, Christenson 365 CONN, India

Cochleanthes discolor (Lindl.) Schultes & Garay, Christenson 436 CONN, Costa Rica

Coelogyne nitida Lindl., Christenson 1017 CONN, India

Cymbidium aloifolium (L.) Sw., Christenson 384 CONN, ex hort.

Dendrobium aphyllum (Roxb.) Fischer, Christenson 837 CONN, India

Dendrobium nobile Lindl., Christenson 387 CONN, India

Dryadella edwallii (Cogn.) Luer, Christenson 1015 CONN, Brazil

Encyclia cochleata (L.) Lemee, Christenson 1016 CONN, ex hort.

Epidendrum anceps Jacq., Christenson 383 CONN, Florida

Haraella retrocalla (Hayata) Kudo, Christenson 1022 CONN, Taiwan

Laelia autumnalis Lindl., Christenson 366 CONN, Mexico

Luisia teres (Thunb.) Bl. var. *botanensis* (Fuk.) T. P. Lin, Christenson 433 CONN, Taiwan

Malaxis latifolia Sm., Christenson 400 CONN, ex hort.

Malaxis paludosa Sw., Reeves, 18 Aug. 1984 MRD, Minnesota

Malaxis unifolia Michx. Reeves, sin., 19 Aug. 1984 MRD, Minnesota

Masdevallia caudata Lindl., Christenson 379 CONN, Colombia

Phalaenopsis lueddemanniana Reichb. f., Christenson 391 CONN, Philippines

Pleurothallis janetiae Luer, Christenson 1014 CONN, Costa Rica

Restrepia striata Rolfe, Christenson 1018 CONN, ex hort.

Rudolfiella aurantiaca (Lindl.) Hoehne, Christenson 386 CONN, Brazil

Sacoila lanceolata (Aubl.) Garay, Christenson 1013 CONN, Florida
Schoenorchis fragrans (Par. & Reichb. f.) Seid. & Smit., Christenson 1019 CONN, India
Thrixspermum saruwatarii (Hayata) Schltr., Christenson 1021 CONN, Taiwan
Tricophilia marginata Henfr., Christenson 380 CONN, Guatemala
Zygostates alleniana Kraenzl., Christenson 1020 CONN, Brazil

THE CORYPHOID PALMS: PATTERNS OF VARIATION AND EVOLUTION[1]

John Dransfield,[2] *I. K. Ferguson,*[2] *and Natalie W. Uhl*[3]

ABSTRACT

Within members of the palm subfamily Coryphoideae are to be found a larger number of unspecialized character states than anywhere else within the Palmae; these include primitive leaf forms, flowers, and pollen. Of the three coryphoid tribes, Corypheae are the least specialized; Phoeniceae occupy an intermediate position; and Borasseae appear to be the most specialized. The pollen of Corypheae and Phoeniceae is largely of a generalized monosulcate form, with few differences in exine ornamentation. Such pollen is very similar to a generalized primitive, monocotyledonous type. Pollen of Borasseae, in contrast, shows specialization. Coryphoid pollen is compared with that of other subfamilies and with putative early monocotyledonous pollen from the early Cretaceous. Aspects of leaf morphology, such as the great variation in the position of the splits and the hastula, are discussed and possible trends of leaf evolution proposed. The position of the palms within the monocotyledons is considered.

A new classification of the palms has recently been completed. An outline of the classification was published by Dransfield & Uhl (1986) in order to validate the names of new suprageneric categories. The basis for the classification is discussed in detail in *Genera Palmarum: A Classification of Palms Based on the Work of H. E. Moore Jr.* (Uhl & Dransfield, 1987). In the new treatment, the palms are divided into six subfamilies: Coryphoideae, Calamoideae, Nypoideae, Ceroxyloideae, Arecoideae, and Phytelephantoideae. The most important characters used in the separation of the subfamilies are the nature of the leaf (whether palmate, pinnate, or bipinnate, and whether induplicate or reduplicate), the inflorescence and its bracts, the arrangement of flowers on the rachillae, floral structure, and the nature of the fruit. The development of the new classification was greatly influenced by a detailed survey of characters (Moore & Uhl, 1982), where the authors have summarized the major trends of evolution in the palms and suggested directions of change in character states.

The greatest concentration of character states believed to be unspecialized (Moore & Uhl, 1982) is found in the Coryphoideae. These include the least specialized inflorescences, the least complex flower groupings, and the only apocarpic palms apart from *Nypa* (Nypoideae). Moore & Uhl (1973) identified the least specialized extant palms as the genera of the apocarpic *Trithrinax* alliance (Moore, 1973), those genera making up subtribe Thrinacinae (Coryphoideae: Corypheae) (Dransfield & Uhl, 1986). Moore & Uhl (1973) pointed out that palms retain many characters considered primitive for the monocotyledons as a whole, but emphasize that they do not suggest linear derivation of all monocotyledons from palms.

The present paper discusses two aspects of the evolution of palms, pollen, and the leaf, by reference to their manifestation in subfamily Coryphoideae.

As circumscribed by Dransfield & Uhl (1986), the Coryphoideae are distinguished by the following characters. The leaves are palmate or costapalmate, rarely entire, induplicate, rarely reduplicate (then with the flowers apocarpous), or mixed induplicate-reduplicate, or pinnate (then the leaflets with entire tips). The flowers may be solitary or clustered; they are never arranged in triads of one central pistillate flower and two lateral staminate flowers. The combinations of these characters allow separation from other subfamilies, but their diffuseness and exceptions indicate the great variability in the subfamily, which includes about 400 species in 39 genera arranged in three tribes: Corypheae, Phoeniceae, and Borasseae. The least specialized tribe, Corypheae (31 genera), is distinguished by the palmate leaf; by genera being

[1] We are grateful to Miss Caroline Batchelor (Coventry (Lanchester) Polytechnic) for carrying out much of the preparation and electron microscopy of the pollen of the Corypheae and Phoeniceae during a one-year undergraduate (Sandwich Course) studentship at the Royal Botanic Gardens, Kew. We also acknowledge her technical help in making up the pollen plates, and we thank Andrew McRobb of the Photographic Unit (Kew) for printing the micrographs.

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hermaphrodite, polygamous, or very rarely strictly dioecious; by the not or only slightly dimorphic flowers; and by the rachillae lacking pits. Tribe Phoeniceae (1 genus), intermediate in specialization, is distinguished by apocarpic flowers and a pinnate leaf with basal leaflets modified as spines. Tribe Borasseae (7 genera), the most specialized of the coryphoid tribes, is distinguished by being strictly dioecious, by the staminate and sometimes also the pistillate flowers borne in deep pits on the rachillae, and by usually strongly dimorphic flowers.

The Corypheae are divided into four subtribes on the basis of the degree of fusion of the carpels. Subtribe Thrinacinae contains 14 apocarpous genera. Subtribe Livistoninae, with twelve genera, has gynoecia of three carpels, free at the base but joined throughout their styles. In subtribe Coryphinae, with four genera, the carpels are basally fused with free or connate styles but often with separate stylar canals. In subtribe Sabalinae, the single genus *Sabal* has carpels joined throughout, the stylar region with a single stylar canal.

Pollen of Coryphoideae

Although the pollen morphology of the Palmae has been surveyed by various workers over the last 20 years (Punt & Wessels Boer, 1966a, b; Thanikaimoni, 1970a, b; Sowunmi, 1972; Kedves, 1981), virtually no electron microscopy of the pollen has been attempted. In fact, the paucity of published electron micrographs of palm pollen is remarkable and commented on by Zavada (1983). Recently the present authors have started a program at Kew to study palm pollen using light and electron microscopy, and some of the results of these studies have been published (Ferguson et al., 1983, 1987; Frederiksen et al., 1985; Ferguson, 1986; Mendis et al., 1987; Harley, 1989).

The pollen morphology of the Coryphoideae has been studied quite extensively with light microscopy (see Thanikaimoni, 1970a; Sowunmi, 1972). Very recently the pollen of tribe Borasseae has been studied in detail with electron microscopy (see Ferguson et al., 1987).

The pollen grains of tribes Corypheae and Phoeniceae are generally monosulcate, elliptic to subcircular in polar view, small to medium in size with L = 20–52 μm, l = 18–45 μm, and h = 12–34 μm (the terminology L, l, h follows Thanikaimoni, 1970a). The apertures are elliptic or rarely subcircular, and very rarely trichotomosulcate, more or less equal in length to the longest axis, and covered with a very thin smooth membrane. The genus *Chamaerops* has pontoperculate apertures. The tectum is reticulate perforate, or foveolate. The exine is usually 1–2 μm thick; some species of *Pritchardia* have thicker walls up to 3 μm, while *Colpothrinax* has pollen with a very thick exine of 3–5 μm. In Corypheae and Phoeniceae the exine stratification is simple with a well developed tectum (which is often relatively thick), columellate layer, and foot layer. The columellae may be arranged in single, double, or many rows supporting the tectum. This character seems to vary within pollen of the same species (Thanikaimoni, 1970a) and does not appear to have any taxonomic significance.

In the tribe Borasseae, four genera have pollen very similar to that of the two preceding tribes, but very large pollen size and monoporate apertures occur. Also there is a very coarse reticulate tectum and supratectal gemmate ornamentation present.

Tribe Corypheae

THRINACINAE. Although there is relatively little variation in the pollen morphology of the genera in subtribe Thrinacinae, a number of small distinctive features are present. The tectum of some genera, including *Coccothrinax* (Figs. 1, 2) and *Maxburretia*, is perforate or occasionally foveolate. *Rhapis*, *Schippia*, *Thrinax* (Figs. 3, 4), *Trithrinax*, and *Zombia* have similar but finer or smaller tectal structures. *Chamaerops* has very remarkable pontoperculate pollen (Figs. 6, 7) and *Cryosophila* sometimes has pollen with trichotomosulcate apertures. In *Chelyocarpus* and *Cryosophila* (Figs. 10, 11) the tectum on the nonapertural side is reticulate, while it is perforate on the apertural side or even complete adjacent to the aperture margins. *Trachycarpus* has pollen with a reticulate or coarsely reticulate tectum with fine granules in the lumina. In this genus also the reticulum is finer on the apertural side than on the nonapertural side. Fine granules are present in the lumina of the reticulate tectum of *Guihaia* and *Cryosophila*.

LIVISTONINAE. The pollen morphology of many of the genera in this subtribe is again of a very generalized monocotyledonous type, and there is a uniformly perforate tectum. This type of pollen is found in *Acoelorraphe*, *Pritchardiopsis*, *Serenoa*, *Brahea*, and *Johannesteijsmannia* (Figs. 15–18). There is a range of variation from a finely perforate tectum to reticulate with small granules in the lumina in *Livistona*; *Licuala* has similar but even greater variation in tectal structure, ranging from finely and sparsely perforate in *L. glabra* Griff.,

for example, to reticulate with isodiametric lumina having dense coarse granules on the nonapertural side in *L.* sp. aff. *peltata* Roxb. (Figs. 8, 9) and with often rather rugulate-perforate aperture margins. *Pritchardia* (Figs. 21, 26) has a sparsely or densely perforate tectum but larger pollen (L = 45–50 μm) than is usual in the subtribe, and the exine is thicker (2–3 μm). Pollen of *Washingtonia* shows a range in tectal perforation with some tendency for smaller lumina on the apertural side and along margins of the aperture in comparison with those on the nonapertural side. The ornamentation of the tectum is somewhat striate-rugulate in *Copernicia* with the muri in more or less parallel rows. *Colpothrinax* has the most distinctive pollen in the subtribe, with differentiation between the tectum of the nonapertural and apertural sides (Figs. 19, 20). Fine granules are present in the lumina. The exine is very thick on the nonapertural side (3–5 μm), where the tectum is thick (Fig. 25).

CORYPHINAE. The pollen of *Corypha* somewhat resembles that of *Colpothrinax* but the exine is thinner (2–3 μm). *Nannorrhops* (Figs. 30, 31) and *Chuniophoenix* (Figs. 34, 36) have pollen similar to that throughout the subfamily. There are very small differences in tectal structure between the species of the two genera.

Kerriodoxa has the most distinctive pollen ornamentation in the subfamily. The muri are discontinuous and form a loosely arranged reticulate pattern on the nonapertural side (Figs. 28, 29). Supratectal granular processes occur on the muri (Figs. 28, 29, 32, 33), and there are fine dense granules in the lumina.

SABALINAE. The pollen of the genus *Sabal* (Figs. 43–46) is of the same general type common throughout the subfamily. The size is generally larger than average (L = ca. 40 μm) and the exine thicker (2–3 μm).

TRIBE PHOENICEAE

The pollen morphology is generally similar to that described in the Corypheae (Figs. 37–42). The tectum is usually distinct on the margins of the aperture from that on the nonapertural side (Figs. 38, 39).

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FIGURES 1–9. 1, 2. *Coccothrinax argentata* (Jacq.) L. H. Bailey (*Small & Carter s.n.*).—1. Whole pollen grain showing apertural side, SEMG (scanning electron micrograph) ×2,200.—2. Exine surface (tectum) on nonapertural side, SEMG ×8,000. 3, 4. *Thrinax parviflora* Swartz (*March 1730*).—3. Whole pollen grain showing nonapertural side, SEMG ×2,900.—4. Nonapertural exine section showing very finely granular tectum, TEMG (transmission electron micrograph) ×20,000.—5. *Coccothrinax rigida* Becc. (*Wright 3220*). Nonapertural exine section, TEMG ×20,000. 6, 7. *Chamaerops humilis* L.—6. (*Moris s.n.*) whole pollen grain showing apertural side with pontoperculum, SEMG ×2,500.—7. (*Brummitt & Ernst 5936*) whole pollen grain exine section with aperture at the top; arrowheads show apertural thinnings on either side of operculum, TEMG ×2,600. 8, 9. *Licuala* sp. aff. *peltata* (*Kerr 11726*).—8. Nonapertural exine section, TEMG ×15,000.—9. Exine surface (tectum) on nonapertural side, showing granules in lumina, SEMG ×8,000.

FIGURES 10–18. 10–13. *Cryosophila warscewiczii* (H. A. Wendl.) H. H. Bartl. (cultivated at Herrenhausen Bot. Gard.).—10. Whole pollen grain showing nonapertural side with coarsely perforate tectum, SEMG ×1,550.—11. Whole pollen grain showing apertural side with a finely perforate tectum in comparison with 10, SEMG ×2,500.—12. Whole pollen grain exine section with aperture at top covered by a very thin aperture membrane (arrowhead). Note the difference in exine surface between the apertural and nonapertural sides. TEMG ×2,300.—13. Nonapertural exine section, TEMG ×20,000.—14. *Cryosophila nana* (Kunth) Bl. ex Salom. (*Langlassé 820*), exine surface (tectum) on nonapertural side, SEMG ×8,000. 15–18. *Johannesteijsmannia*.—15. *J. perakensis* J. Dransf. (*Dransfield 871*), whole pollen grain showing apertural side, SEMG ×3,300. 16–18. *J. altifrons* (Reichb. f. & Zoll.) H. E. Moore (*Dransfield 916*).—16. Whole pollen grain exine section with aperture at top, TEMG ×2,000.—17. Nonapertural exine section, TEMG ×20,000.—18. Exine surface (tectum) on nonapertural side, SEMG ×8,000.

FIGURES 19–27. 19, 20, 25. *Colpothrinax wrightii* Griseb. & H. A. Wendl. (*Wright 3964*).—19. Whole pollen grain showing nonapertural side, SEMG ×1,650.—20. Whole pollen grain showing apertural side, SEMG ×1,650.—25. Whole pollen grain exine section with aperture at top, note differences in tectum between apertural and nonapertural sides (arrowheads), TEMG ×1,600.—21. *Pritchardia minor* Becc. (*Cranwell et al. 3103*), whole pollen grain partly showing apertural and nonapertural sides, SEMG ×1,650.—22. *Washingtonia robusta* H. A. Wendl. (*Palmer 144*), whole pollen grain showing apertural side, SEMG ×1,600. 23, 24. *Livistona* sp. (*Kerr 3430*).—23. Whole pollen grain partly showing apertural and nonapertural sides, SEMG ×2,500.—24. Nonapertural exine section, TEMG ×30,000.—25. See above.—26. *Pritchardia martioides* Rock & Caum (*St. John 10180*), whole pollen grain exine section with aperture at top; note differences in tectum between apertural and nonapertural sides (arrowheads), TEMG ×3,000.—27. *Washingtonia filifera* (Linden) H. A. Wendl. (*Wright s.n.*), whole pollen grain exine section, TEMG ×3,000.

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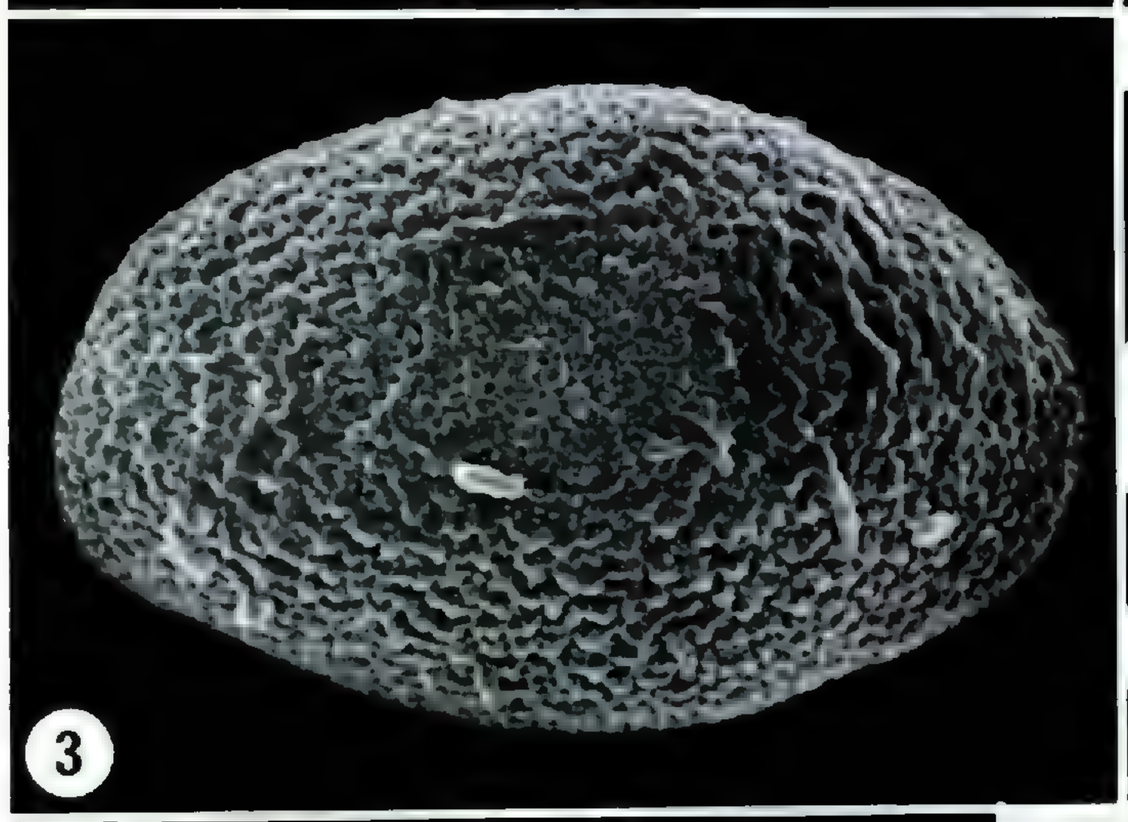
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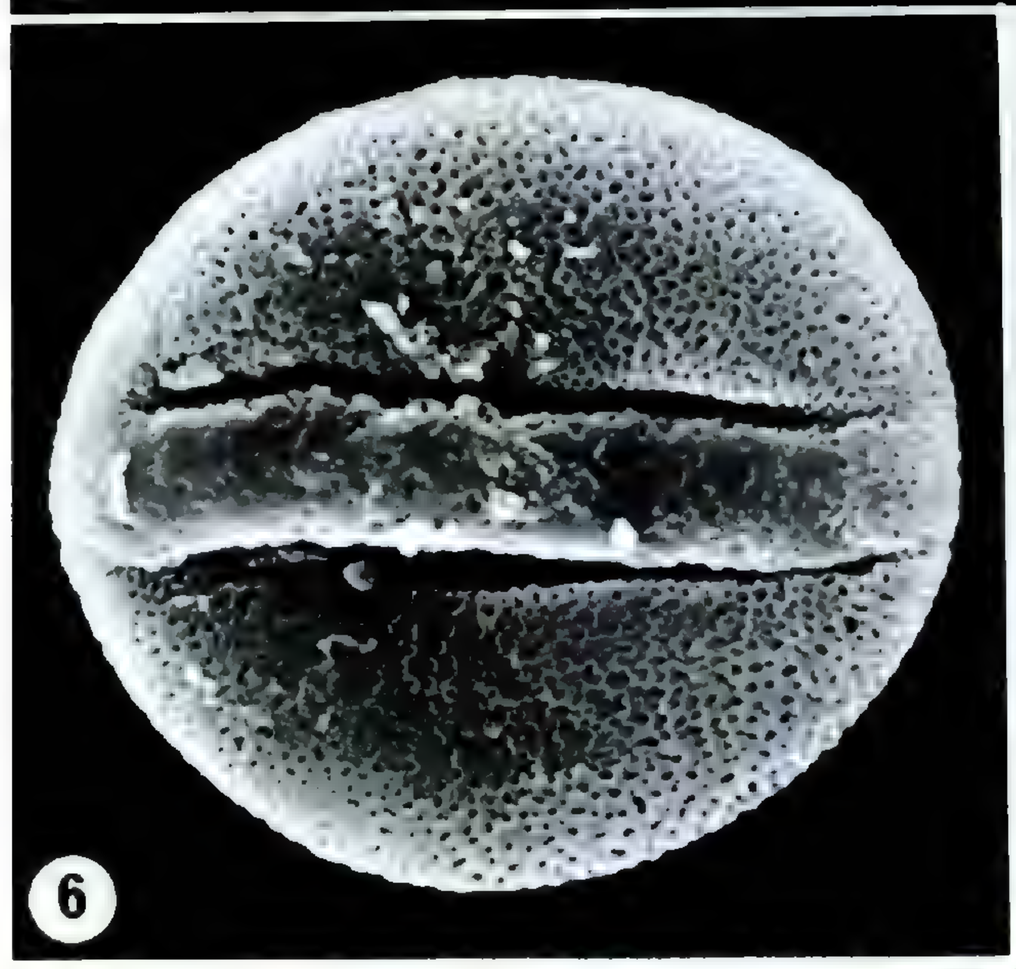
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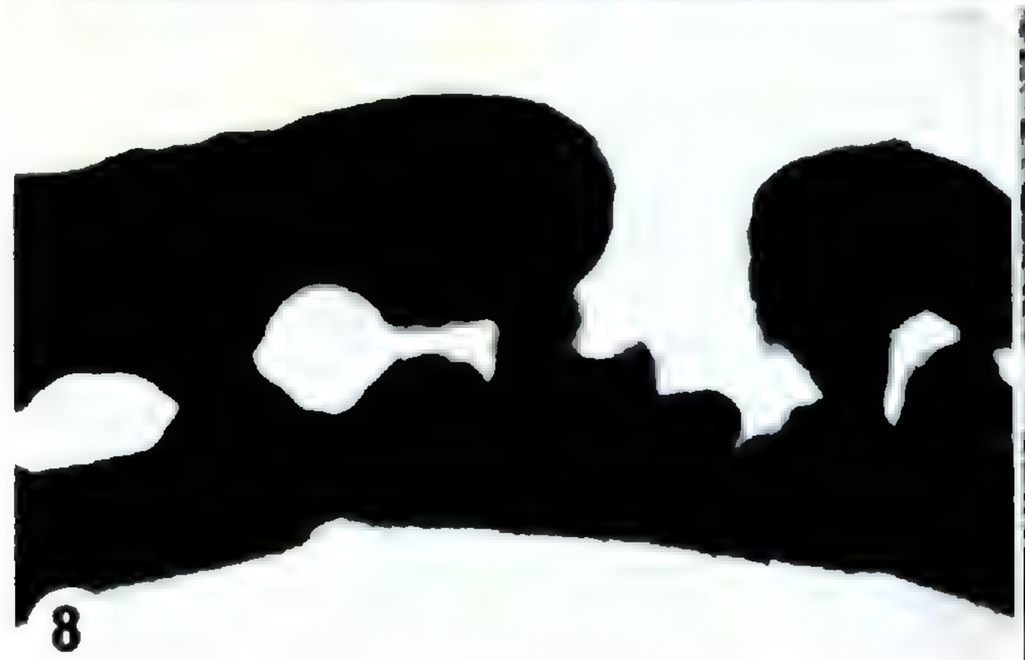
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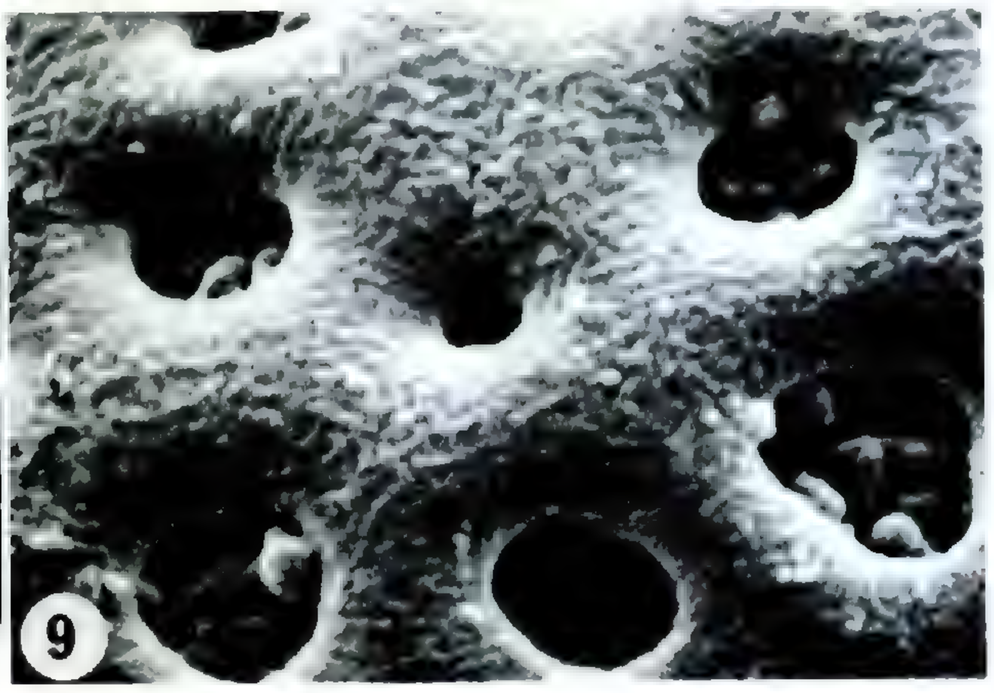
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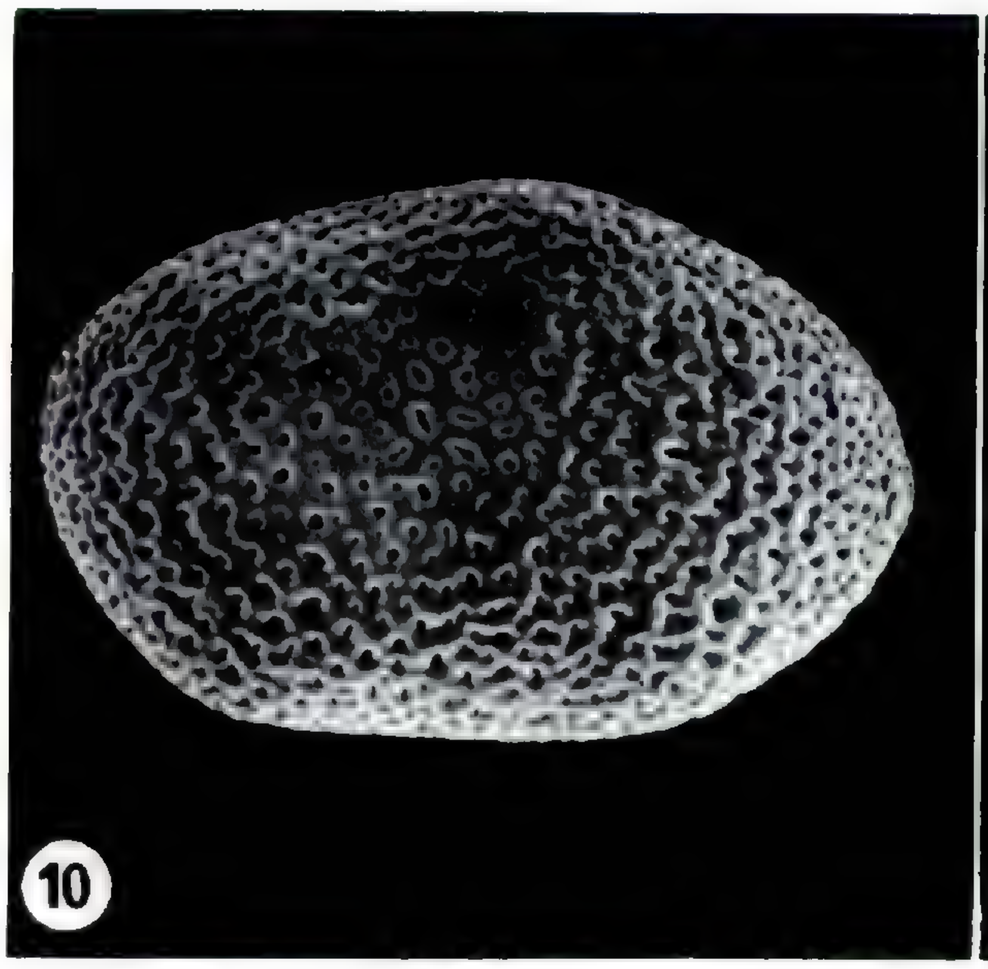
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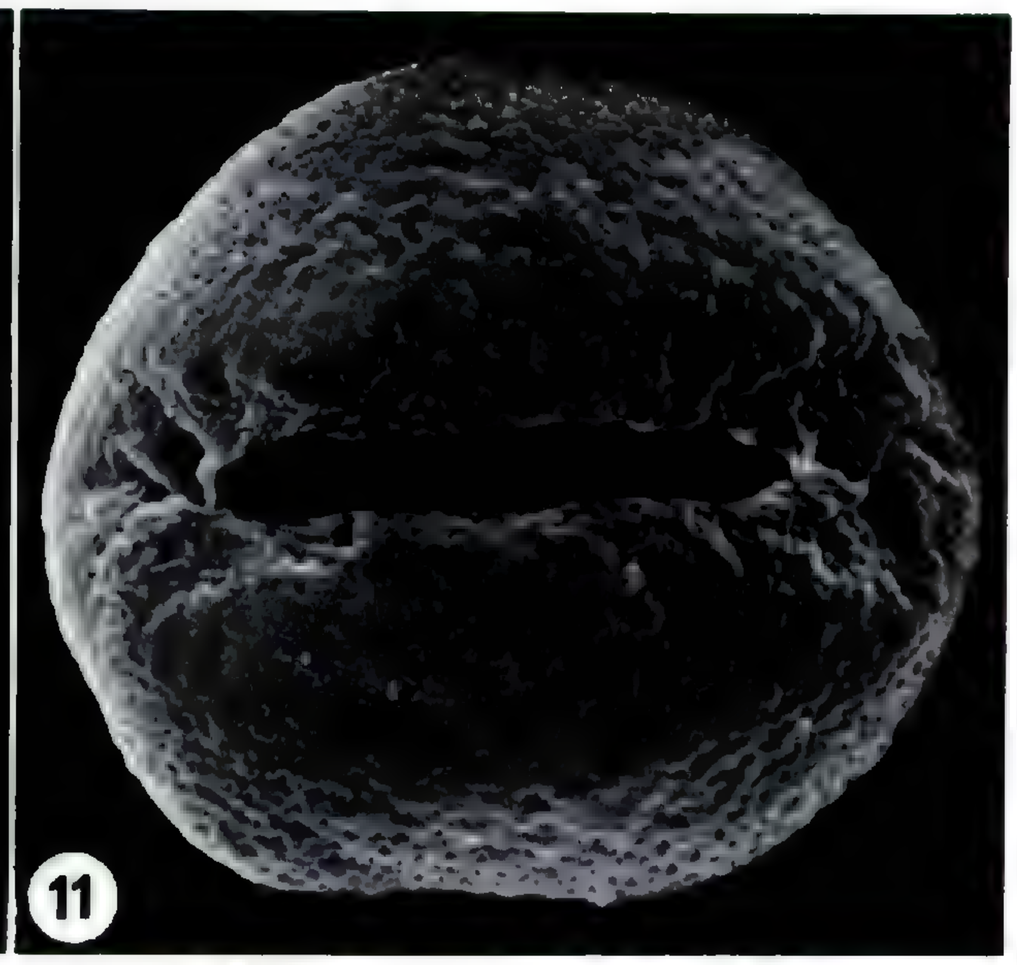
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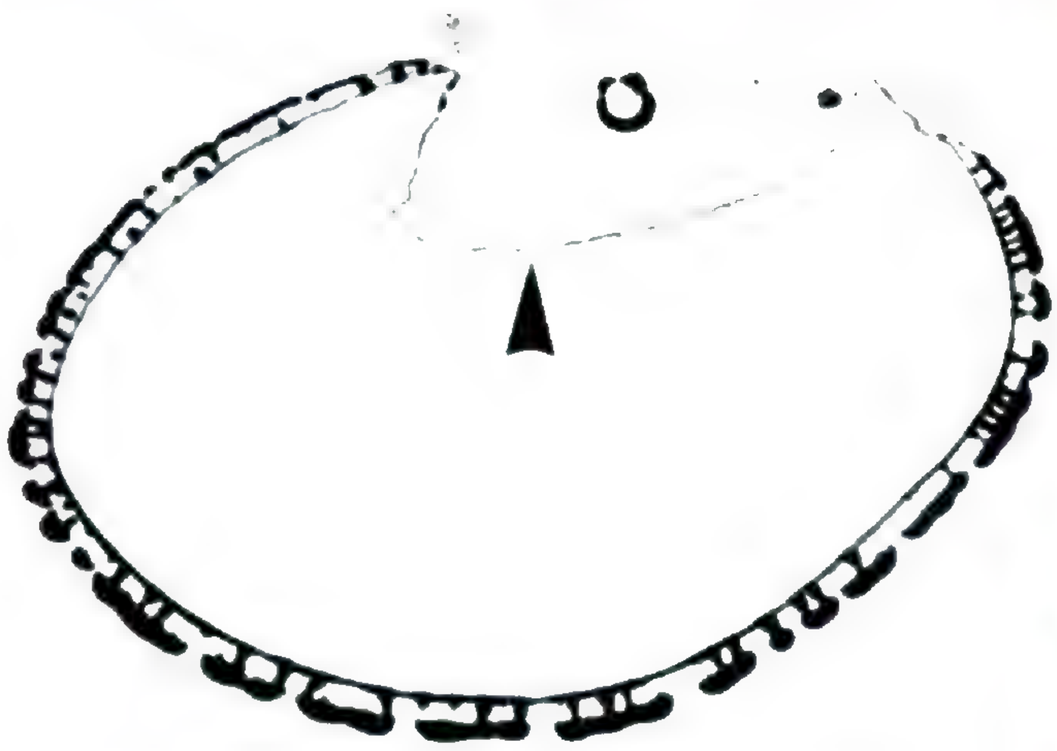
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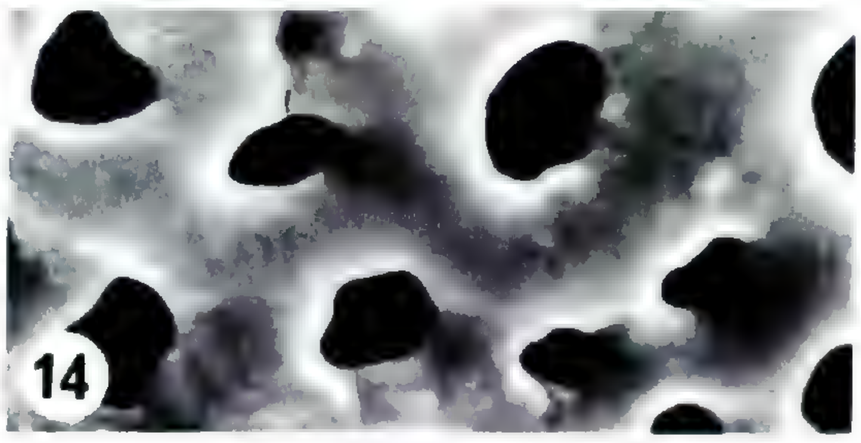
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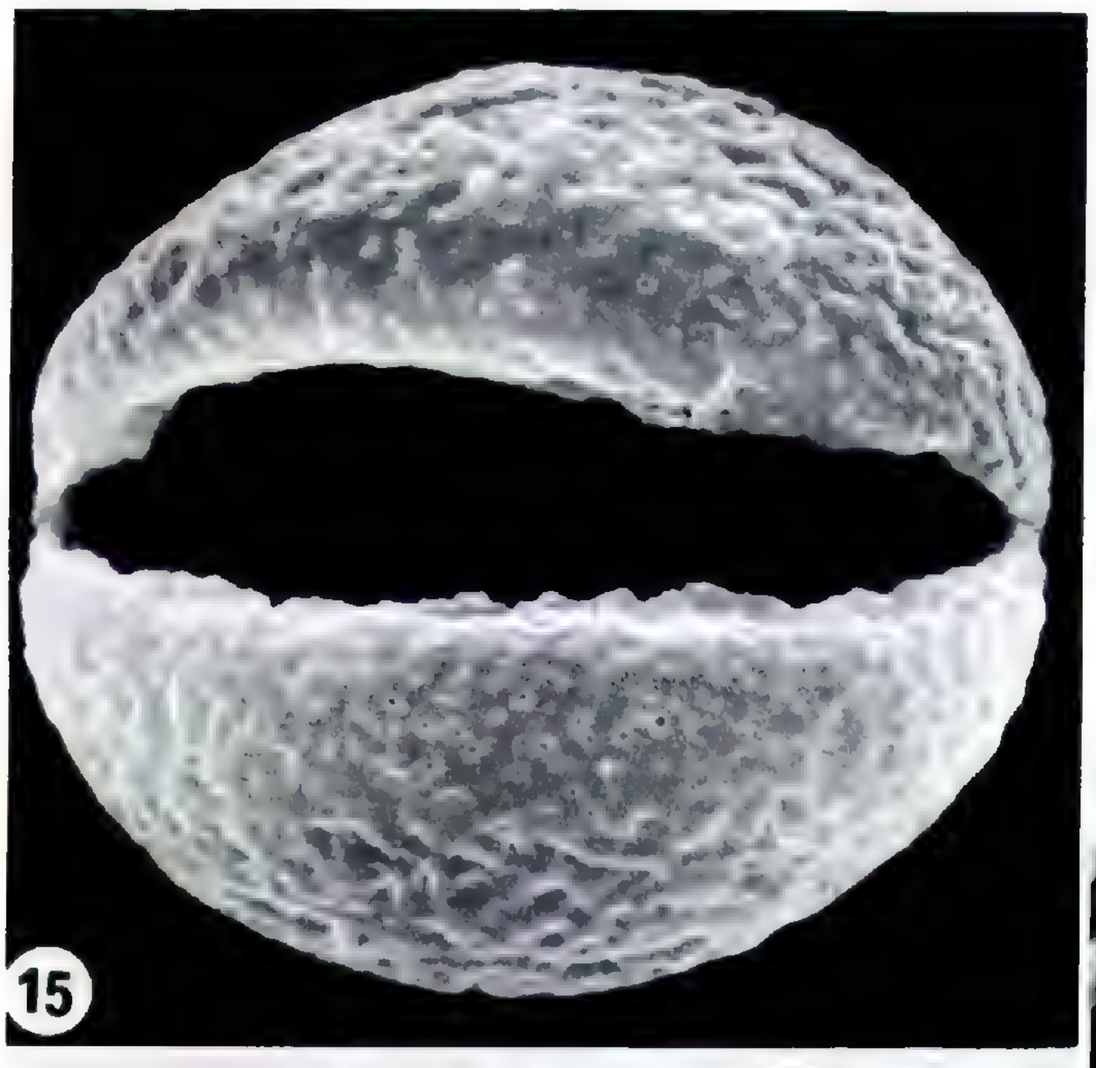
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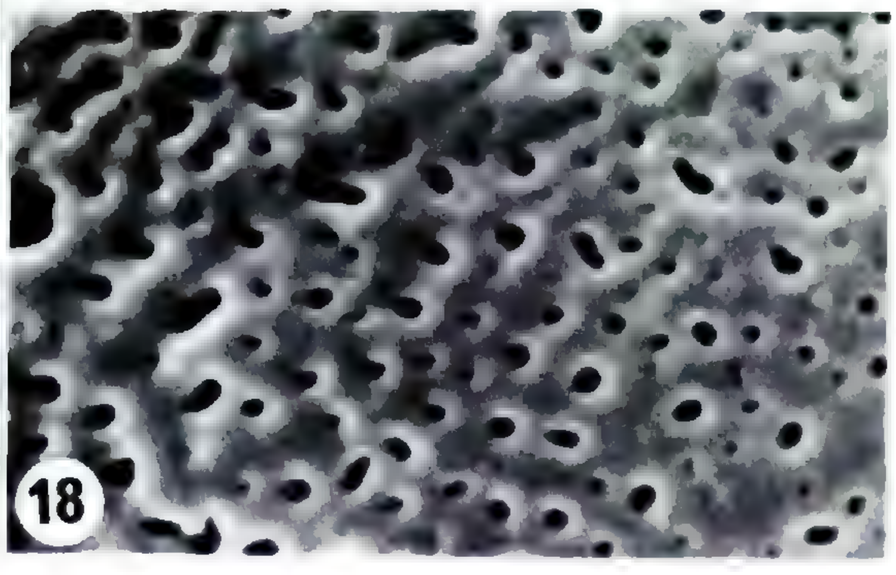
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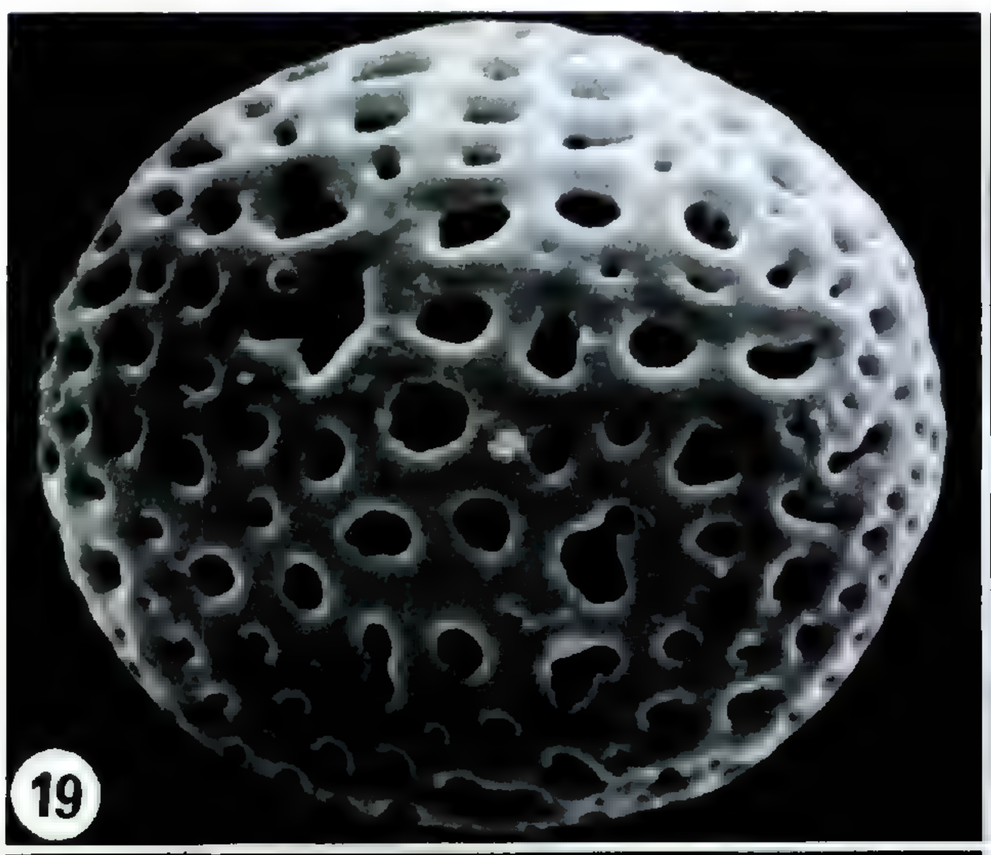
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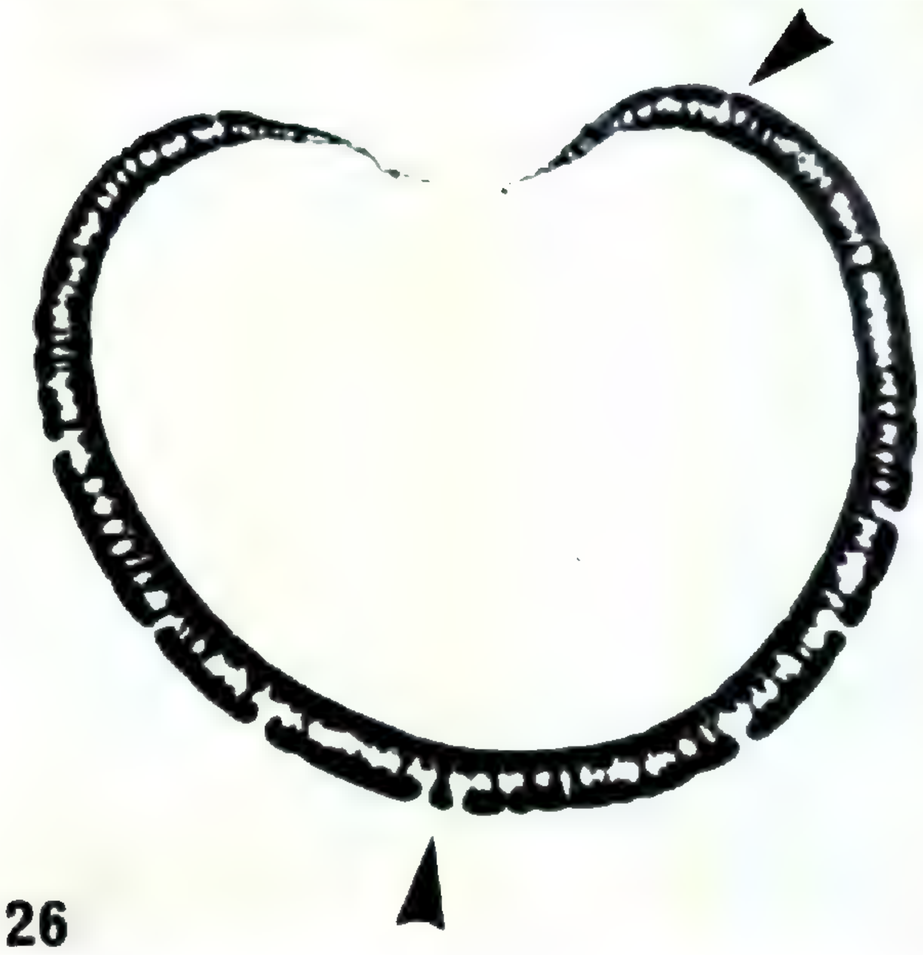
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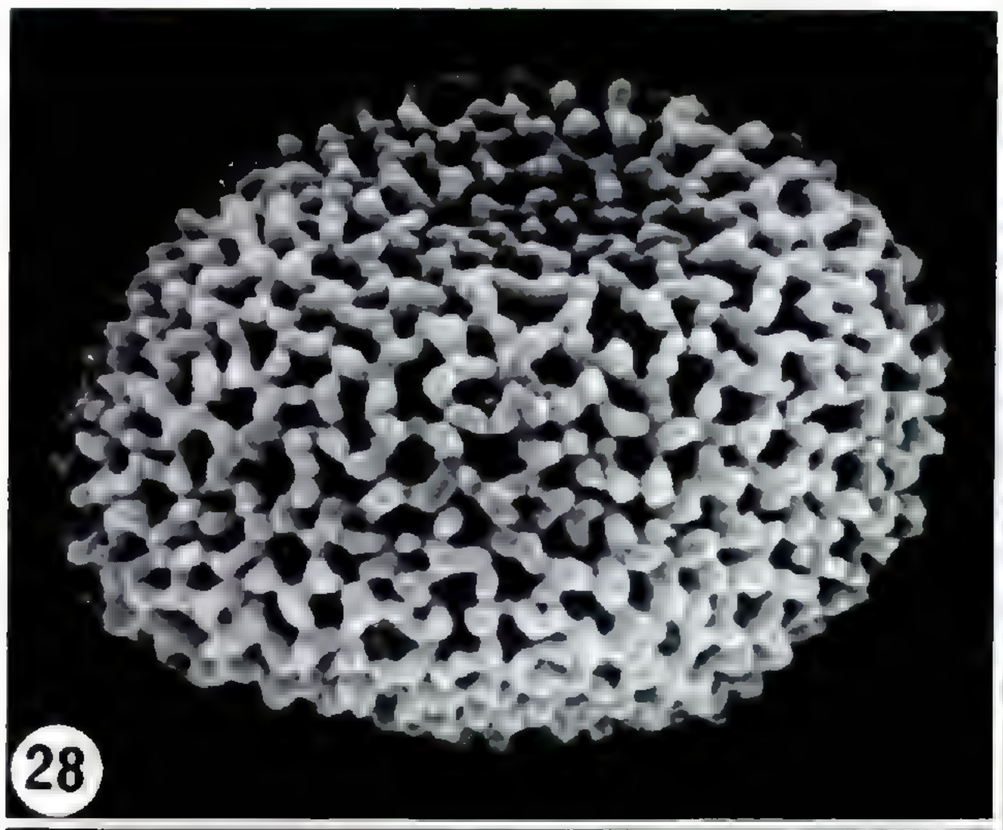

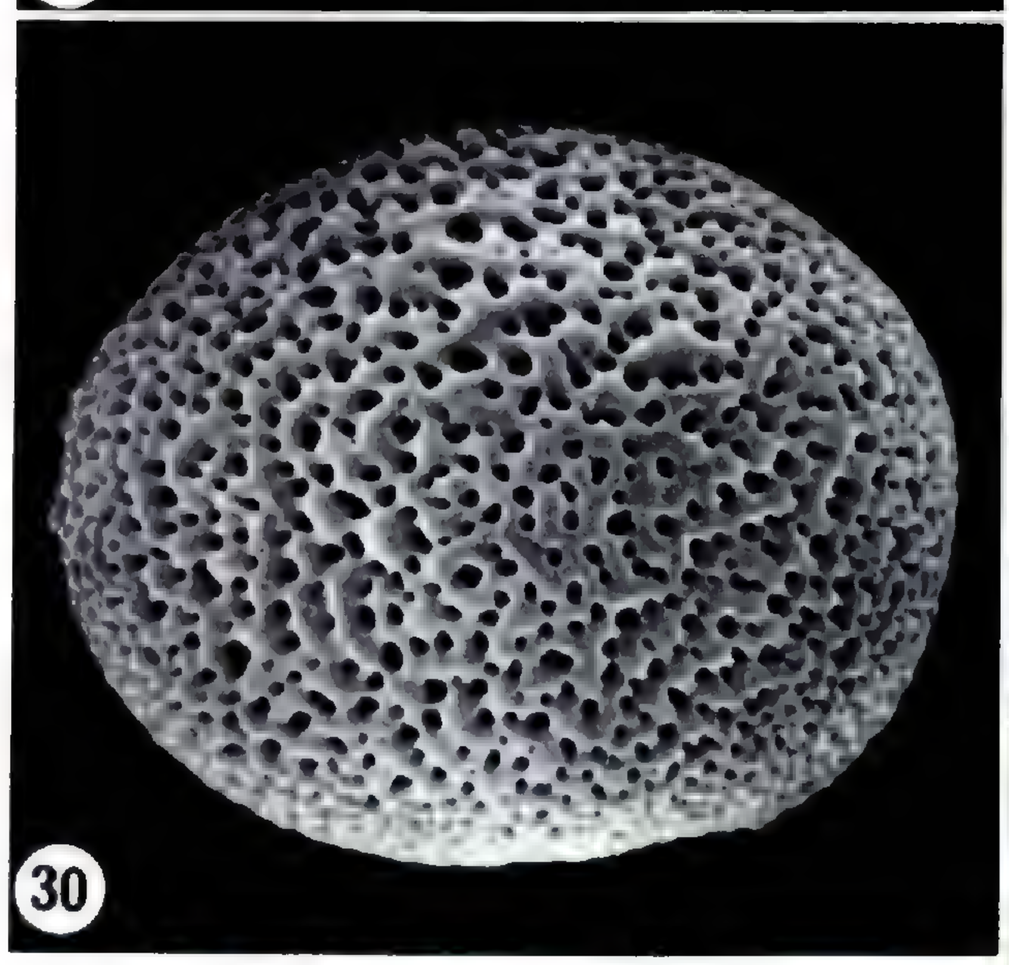

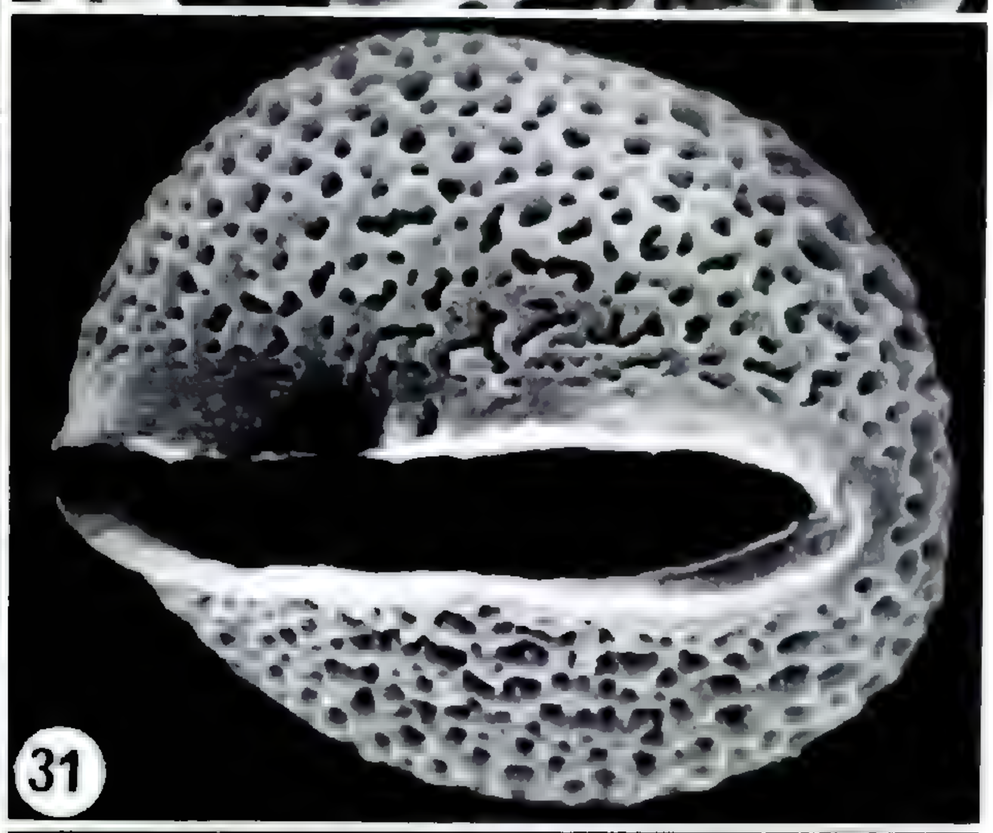

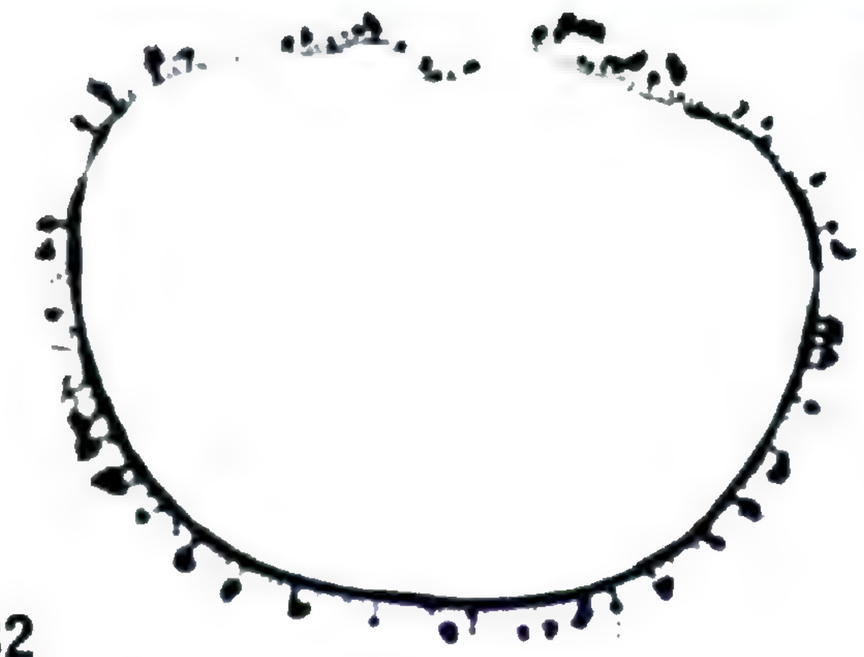

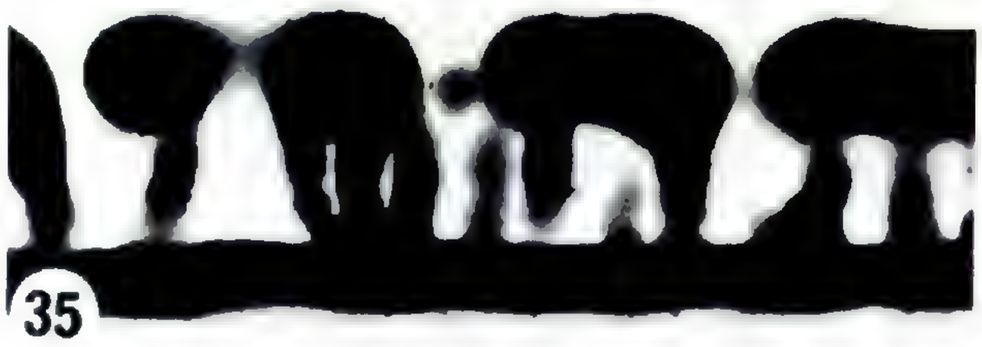

FIGURES 28 36. 28, 29, 32, 33. *Kerriodoxa elegans* J. Dransf. (*Bhoonab s.n.*).—28. Whole pollen grain showing nonapertural side, SEMG ×2,400.—29. Exine surface on aperture margin, SEMG ×8,000.—32. Whole pollen grain section with aperture at top, TEMG ×2,000.—33. Nonapertural exine section, granularlike supratectal processes indicated with arrowhead, TEMG ×20,000.—30. *Nannorrhops ritchiana* (Griff.) Aitch. (cultivated in

TRIBE BORASSEAE

There is more variation in the pollen morphology of the genera of this tribe than in the two preceding (Ferguson et al., 1987). The genera *Latania*, *Lodoicea*, *Medemia*, and *Bismarckia* have pollen of the general type found throughout the subfamily. *Borassus* and *Hyphaene* have pollen with supratectal gemmate processes. *Borassodendron* has very large circular pollen (L = ca. 73 μm, l = ca. 73 μm, h = 72 μm) with very thick walls (4–6 μm). One species, *B. machadonis* (Ridley) Becc., has porate apertures.

Within the subfamily there are few pronounced trends in the pollen morphology, yet tribe Borasseae tends to have more specialized pollen with larger pollen size, porate apertures, and supratectal structures.

Within the other two tribes a slight tendency for increase in pollen size occurs, as does an increase in reticulum size together with the presence of granules in the lumina. These characters may be interpreted as being indicative of a low level of specialization. Likewise, the increase in thickness of the pollen walls and the differences in tectal ornamentation between the apertural and nonapertural sides are perhaps specialized.

Comparison of Coryphoideae Pollen with that of Other Subfamilies

The pollen morphology of Coryphoideae is fairly uniform, and only *Kerriodoxa* and some genera in tribe Borasseae do not conform to a very generalized type. The significance of the pontoperculate pollen of *Chamaerops* (which is paralleled in the small genus *Iriartella* in subfamily Arecoideae) and the distinctive ornamentation in the pollen of *Kerriodoxa* is unclear.

Uniformity of pollen morphology in the Coryphoideae contrasts markedly with that found in the other subfamilies. The monosulcate pollen type with a perforate or reticulate tectum occurs throughout the entire family (Harley, 1990). However, there is a huge range of variation in ornamentation, apertures, and in exine stratification. For example, in the Calamoideae there is intectate gemmate and spinose pollen in *Salacca*, *Daemonorops*, and *Korthalsia* as well as tectate psilate or sparsely perforate tectate pollen in the two former genera (Ferguson, 1986). Extended sulcate, dicolpate, and diporate pollen occurs in *Calamus*, *Salacca*, *Daemonorops*, and *Korthalsia* (Thanikaimoni, 1970a; Frederiksen et al., 1985; Ferguson, 1986). Supratectal spines and supratectal gemmae occur in *Retispatha* and *Calamus*. *Mauritia*, *Mauritiella*, and *Lepidocaryum* have spinose pollen, the spines being characteristically sunk into the foot layer (Sowunmi, 1972; Ferguson, 1986).

Nypa has tectate spinose pollen with an extended sulcus (Thanikaimoni, 1970a; Ferguson, 1986).

In the Ceroxyloideae, *Louvelia* has monoporate pollen (Ferguson et al., 1988), whereas *Ravenea* has tectate spinose pollen (Ferguson, 1986). Trichotomosulcate pollen occurs in *Chamaedorea*, although many species in the genus have pollen resembling closely the generalized type found in the Coryphoideae.

The pollen of the Arecoideae is probably the most varied, although there are many genera with the generalized monosulcate type (Harley, 1990); a very great range of types occurs within the genus *Pinanga* alone (Ferguson et al., 1983). *Areca* has triporate, porate, extended sulcate, and simple monosulcate pollen (Ferguson & Dransfield, unpublished). A mixed granular and columellar interstitium occurs in the monoporate *Areca caliso* Becc. (Ferguson & Dransfield, unpublished). *Sclerosperma* also has triporate pollen (Thanikaimoni, 1970a). Trichotomosulcate grains occur in, for example, *Pinanga*, *Elaeis*, *Bactris*, *Astrocaryum*, and *Acrocomia* (Thanikaimoni, 1970a; Sowunmi, 1972; Ferguson, 1986; Ferguson & Dransfield, unpublished). Intectate gemmate pollen is present in *Arenga*, *Caryota*, and *Dictyocaryum* (Ferguson, 1986). *Socratea*, *Catoblastus*, and *Wettinia* have large spines interspersed with dense granular spinules (Ferguson, 1986).

Comparisons with the Fossil Record

Comparison of the pollen morphology of the Coryphoideae with putative fossil monocotyledon-

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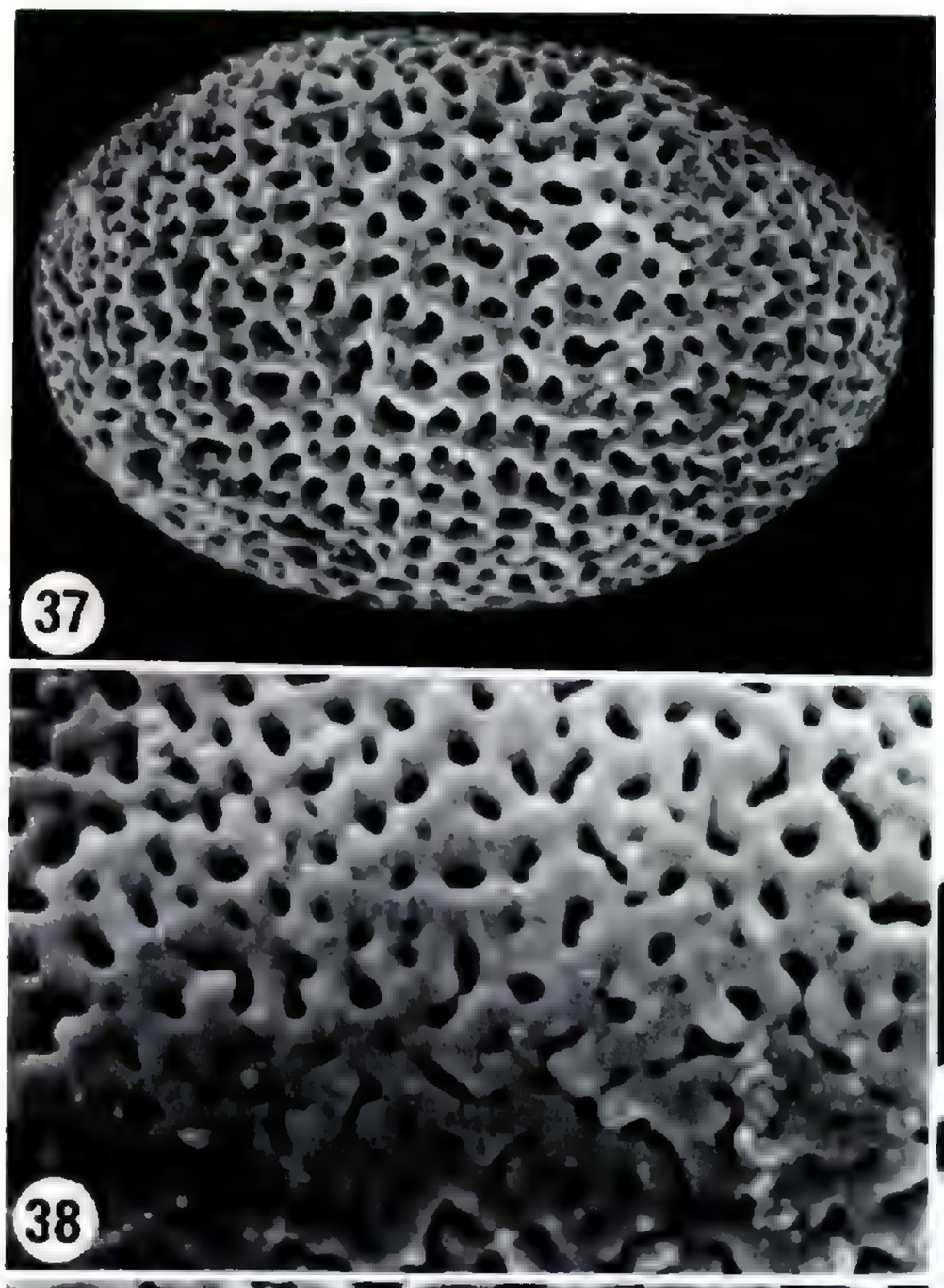
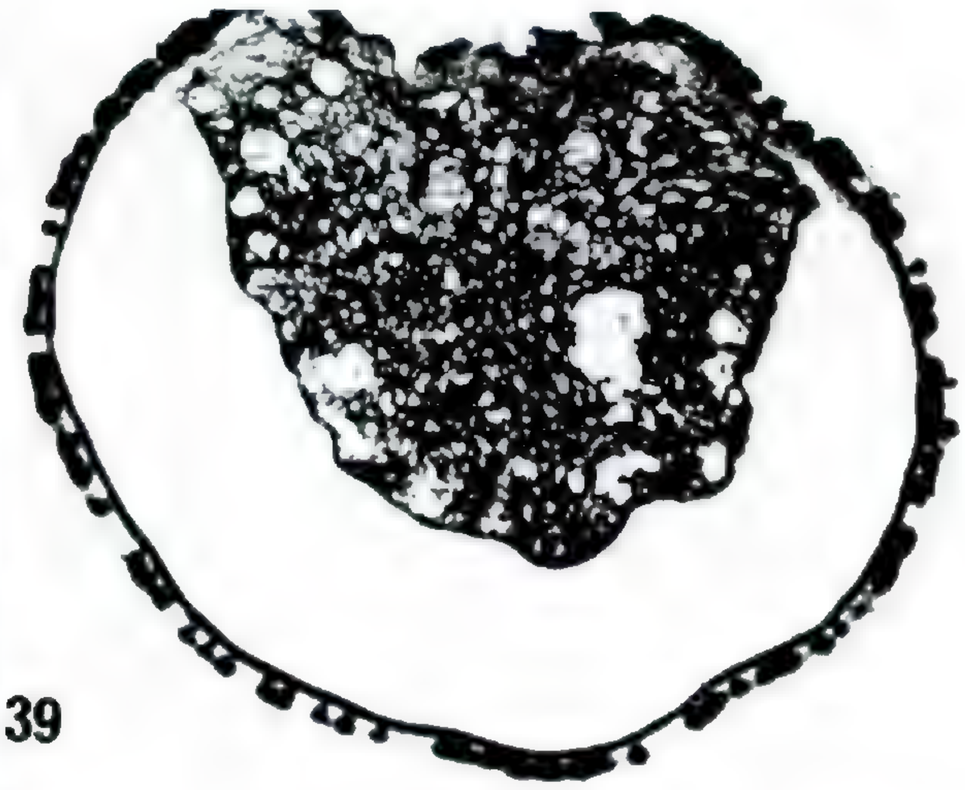
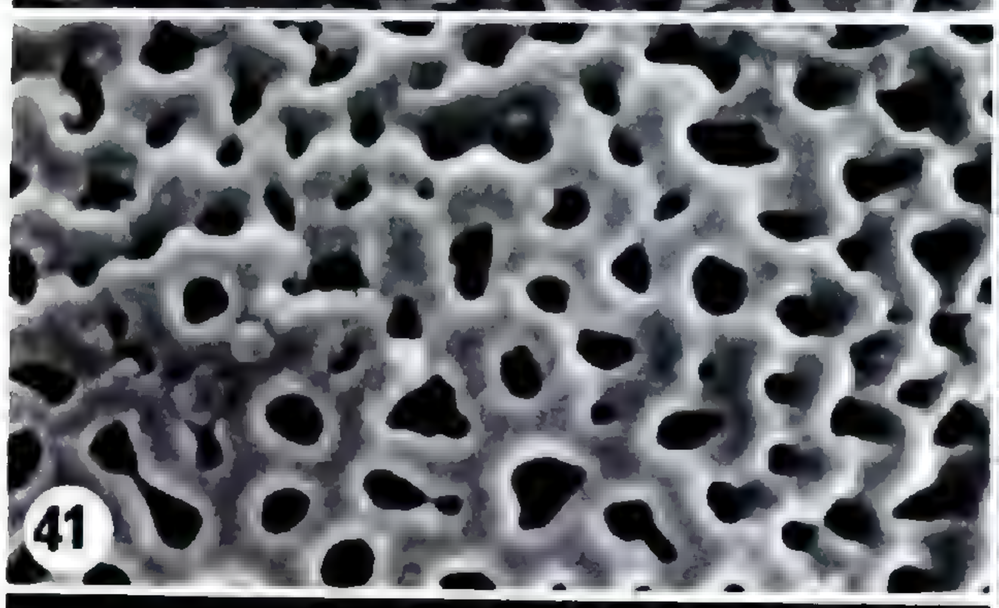
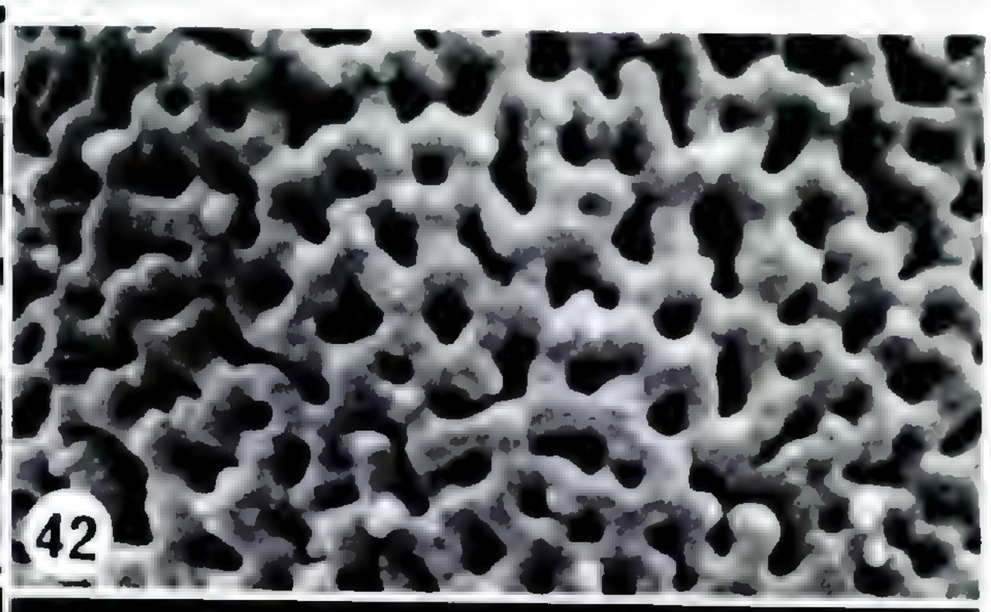
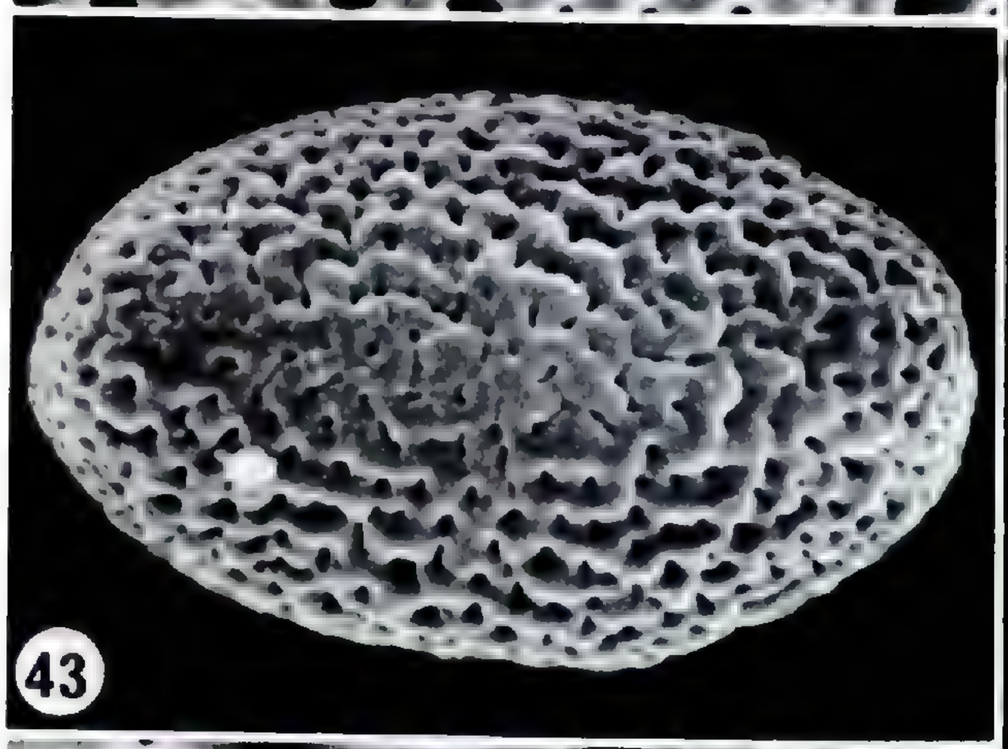
India—Saharanpur), whole pollen grain showing nonapertural side, SEMG ×2,000.—31. *Corypha umbraculifera* L. (*Thwaites 2336*), whole pollen grain showing apertural side, SEMG ×2,200. 32, 33. See above. 34, 36. *Chuniophoenix hainanensis* Burret (*Whitmore 3152*).—34. Whole pollen grain showing apertural side, SEMG ×2,200.—35. See below.—36. Nonapertural exine section, TEMG ×30,000.—35. *Nannorrops ritchiana* (Griff.) Aitch. (*Radcliffe-Smith 5471*), nonapertural exine section, TEMG ×20,000.

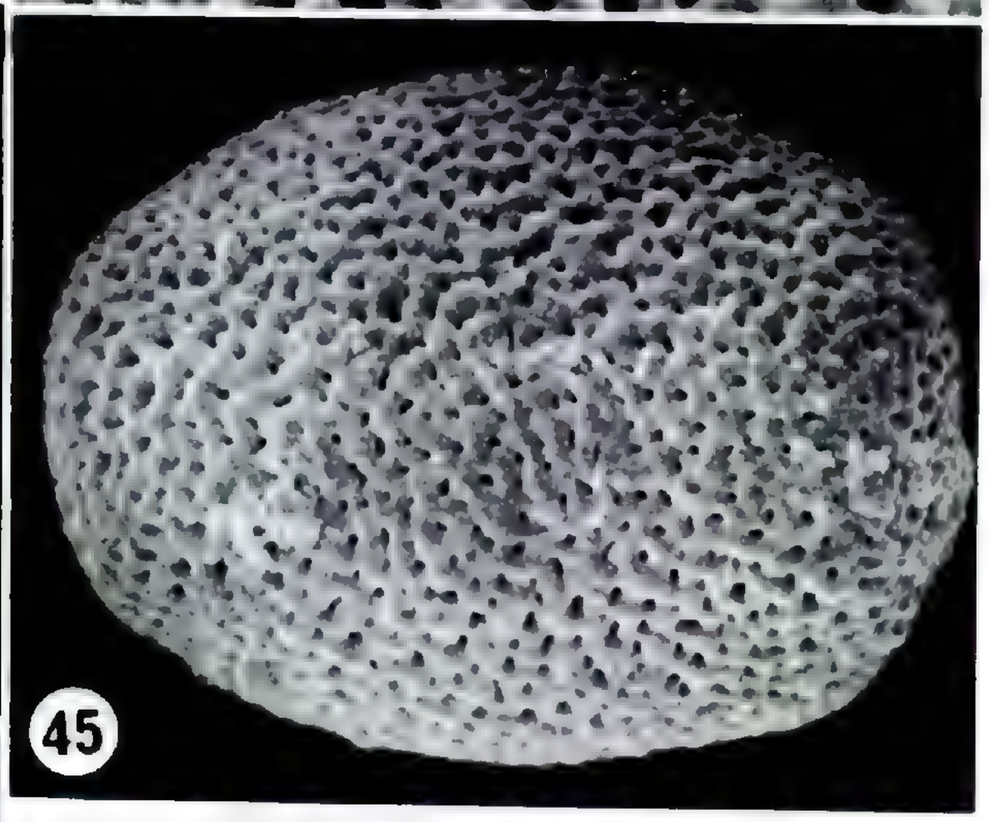


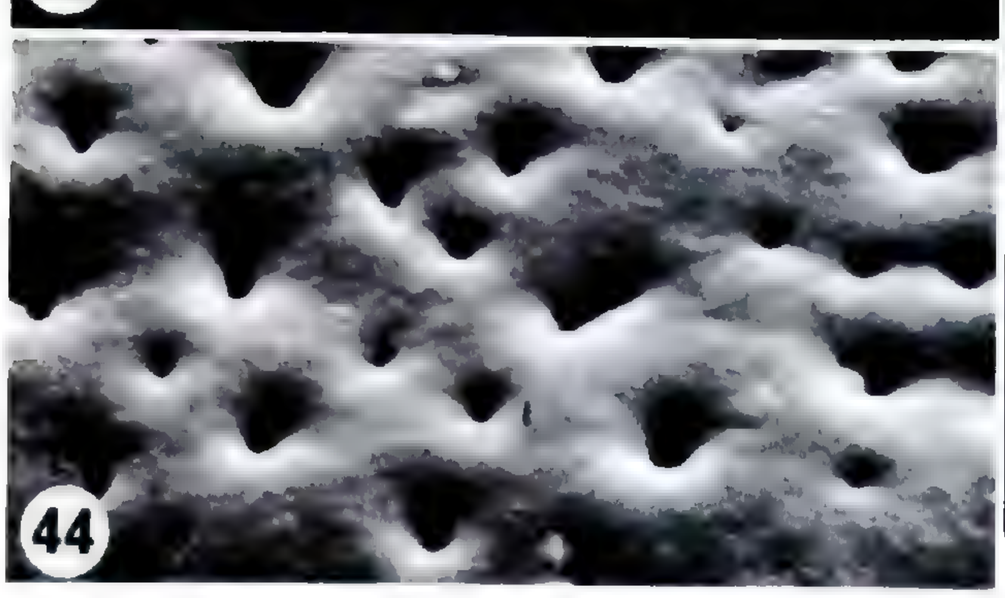


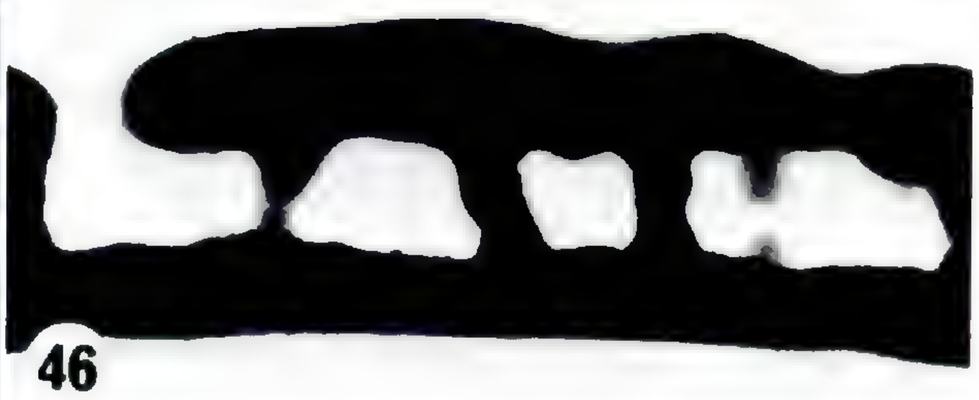












FIGURES 37–46. 37, 38. *Phoenix* sp. (*Kerr 6872*).—37. Whole pollen grain showing nonapertural side, SEMG ×3,000.—38. Exine surface on aperture margin, SEMG ×8,000. 39–41. *Phoenix paludosa* Roxb. (*Schmidt 362*).—39. Whole pollen grain section with aperture at top, some contents remaining after acetolysis, TEMG ×3,700.—40. Nonapertural exine section, TEMG ×36,000.—41. Exine surface (tectum) on nonapertural side, SEMG ×8,000.—42. *Phoenix dactylifera* L. (*Guiaro 2314*), exine surface (tectum) on nonapertural side, SEMG

ous pollen suggests that there are very close similarities between those of the *Liliacidites–Retimonocolpites* type pollen and the pollen of subfamily Coryphoideae. Pollen types, some remarkably similar to those of Coryphoideae, are described by Doyle (1973) and Walker & Walker (1985, 1986) from the Lower Cretaceous Potomac Group of North America. The more coarsely reticulate *Clavatipollenites* grains are not so readily matched among the Coryphoideae. The differences in tectum between the apertural and nonapertural sides in extant palm pollen might prove to be of value in relating the pollen of Coryphoideae to fossil pollen types. It is perhaps noteworthy that the trichotomosulcate apertures occurring in early fossil deposits are relatively rare in Coryphoideae but widespread in other subfamilies of the palms. Likewise, the very coarsely reticulate ornamentation like that in early fossils (*Retimonocolpites*) occurs in the Arecoideae (*Nenga* and *Gronophyllum*, for example) but is absent from the Coryphoideae. There are also faint similarities between the pollen of *Kerriodoxa* and some *Clavatipollenites* types with ridged or granular structures on the muri.

It can be postulated that the pollen morphology of the Coryphoideae is unspecialized. This view is supported by other morphological characters and from comparison with the fossil record where similar types have been shown to occur in the Lower Cretaceous (Walker & Walker, 1985, 1986). The pollen morphology of the other subfamilies is much more variable and can be regarded as being more specialized, and appears much later in the fossil record, extending from the Maestrichtian, but is much more frequently found in Eocene and Miocene deposits (Muller, 1980, 1981).

Identification of Coryphoideae pollen in the fossil record seems likely to be very difficult because it is so very similar to the relatively commonly occurring and widespread monocotyledonous generalized type. However, we stress that, although it may be impossible to equate such early pollen types with palms positively, it may be equally impossible to rule palms out.

The Leaf of Coryphoideae

The plicate and usually split leaf is the most distinctive organ of the palm family and more than any other structure links palms together. Such plicate leaves are scattered in other monocotyledonous families, but outside of the palms splitting of the plicate leaf is found only in some members of the Cyclanthaceae and in *Curculigo seychellensis* Bojer (Hypoxidaceae). The structure of the leaves of Cyclanthaceae has been the subject of recent investigations by Wilder (1976, 1981). In *Curculigo seychellensis*, the leaf blade is borne on a spiny petiole and is deeply bifid down the midline at maturity, thus presenting a remarkably palmlike appearance (Dransfield, pers. obs.); this is the only member of the genus to possess a split leaf.

Palm leaves, as is well known, may be palmate, costapalmate, pinnate, bipinnate, or entire and pinnately or palmately ribbed. The blade is always plicate in bud and the folds are usually prominent in the mature leaf, although occasionally very indistinct, as in some species of *Chamaedorea*. The origin and development of the plications, for long a mystery and the source of much speculation, has recently been elucidated by Kaplan et al. (1982).

In some previous classifications of the family (e.g., Satake, 1962; Saakov, 1954), the nature of the splitting, whether along the adaxial or abaxial folds, has been considered to be of fundamental importance. In the most recent classification (Dransfield & Uhl, 1986; Uhl & Dransfield, 1987), although the position of the splits is largely consistent with division of the family based on other characters, there are some exceptions of great interest, which are almost all to be found within the Coryphoideae. Indeed subfamily Coryphoideae has a wider range of leaf form than any other of the six palm subfamilies (Dransfield & Uhl, 1986). Yet this great range has perhaps not been fully appreciated in the past, and contrasts markedly with the general uniformity in pollen morphology.

Most members of Coryphoideae have palmate or costapalmate leaves with blades partially divided along the adaxial folds into induplicate segments. Costapalmate leaves differ from strictly palmate leaves in the presence of a costa, an extension of the petiole into the blade, representing the true midrib of the whole leaf. Entire undivided leaves are quite common in juvenile stages of many coryphoid genera but at maturity occur only in *Johannesteijsmannia* and a few species of *Licuala*, e.g., *L. grandis* H. A. Wendl. and *L. orbicularis* Becc. Pinnate leaves are found only in *Phoenix*, the only genus in tribe Phoeniceae.

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×8,000.—43. *Sabal mexicana* Mart. (*Palmer 193*), whole pollen grain on nonapertural side, SEMG ×1,650.—44. *Sabal yapa* Wright ex Becc. (*Gentle 1156*), exine surface (tectum) on nonapertural side, SEMG ×8,000. 45, 46. *Sabal palmetto* Lodd. ex Schult. (*Fredholm 5390*).—45. Whole pollen grain on nonapertural side, SEMG ×2,000.—46. Nonapertural exine section, TEMG ×15,000.

Until recently the division of the leaf blade in Coryphoideae was considered to be consistently into induplicate segments. It is now known that several types of splits occur in the subfamily. We can distinguish splits along the adaxial folds, along the abaxial folds, and between-fold splits. Splits may be shallow or deep, or may even reach the insertion of the blade on the petiole or costa. Preliminary investigations of the development of the leaves suggest that the various types of splitting occur at different times during development and that the types of splitting are not equivalent (Dransfield, 1970). The diversity of leaf form within the subfamily is caused by combinations of the several types of split. Elsewhere in the family, there is diversity of leaf form but, except in Arecoideae (where adaxial splits occur), the range of splitting mechanisms appears not to occur. Still much work needs to be done on the different forms of pinnate leaves.

The simplest form of blade in the subfamily is exemplified by *Chamaerops humilis* L. and many other genera and species; in this type the blade is regularly divided along the adaxial ribs to about half the blade radius into single-fold, induplicate segments, which in turn are divided shallowly along the abaxial rib. Splitting of the blade occurs relatively late in the development of the leaf and is completed by expansion of the sword leaf from the apical bud. Splitting seems to be intimately associated with the mechanical forces of the expanding leaf. The leaf of *Trachycarpus fortunei* (W. J. Hook.) H. A. Wendl. is only slightly different: the divisions of the blade are unequal and the resulting segments are of differing lengths. Most costapalmate leaves have blades divided rather regularly into single fold segments of similar length, but in some taxa, such as all members of the genus *Pholidocarpus* and *Livistona saribus* (Lour.) Merr. ex Chev., the blade is divided by a few very deep adaxial splits into many fold segments, which are in turn divided along adaxial folds by shorter splits into single fold segments. The timing of the deeper splits in relation to the shallow splits has not been investigated.

Many members of tribes Corypheae and Borasseae have rather strongly costapalmate leaves. In some costapalmate leaves, such as those of *Livistona decipiens* Becc. and *L. loriphylla* Becc., the splits in the distal part of the leaf may nearly reach the costa; the distal part of the leaf resembles the leaf of *Phoenix* and suggests perhaps how the leaf of *Phoenix* may have evolved. However, leaf development in *Phoenix* is strikingly different (see below).

Splitting along the abaxial folds occurs in a few genera. In *Guihaia* the blade is divided to about ½–¾ the radius into neat reduplicate segments (Dransfield et al., 1985). This clearly reduplicate palmate-leaved genus is closely related by inflorescence and flower structure to the induplicate palmate-leaved *Maxburretia*. *Guihaia* has the only leaf of its type in the subfamily. Elsewhere in the palms, strictly reduplicate palmate leaves are known only in three calamoid genera, *Mauritia*, *Mauritiella*, and *Lepidocaryum*. In other coryphoid genera displaying abaxial splits in the leaves, the abaxial splits appear to be superimposed on a basically induplicate leaf. In most species of *Cryosophila*, *Chelyocarpus*, and *Itaya* the leaf blade is divided into induplicate segments, but the whole blade is bisected right through to the insertion by a deep split along the central abaxial fold, i.e., along the true midrib of the leaf. The timing of this split has not been examined, but in *Sabal*, some species of which also display this central split, the split occurs early in the development of the leaf, several plastochrons before the adaxial splits occur (Uhl, unpublished). This deep central split is paralleled in many pinnate-leaved palms, in some members of the Cyclanthaceae, and in *Curculigo seychellensis*.

In *Licuala*, apart from the species with entire leaves, the blade is regularly divided right to the insertion along the abaxial ribs. The segments thus produced are usually broadly wedge-shaped and composed of several folds. In most species the individual segments are lobed along the apical margin by short splits of varying depth, longer splits occurring on the adaxial folds, shorter on the abaxial folds. This short lobing thus appears to correspond with the induplicate segments in other coryphoid palm leaves. Furthermore, the deep abaxial splits that divide the leaf into segments occur very early in the development of the leaf, usually by the third plastochron (Dransfield, 1970). This suggests that the splitting mechanism may be different, and is superimposed upon a basically induplicately split leaf. In one species, *L. bidentata* Becc., the segments are sometimes composed of only one fold, and the blade superficially resembles that of the three reduplicately palmate calamoid genera mentioned above. We may regard the entire leaves of *L. orbicularis* and *L. grandis*, which, although not being deeply split, still retain the shallow marginal induplicate lobing, as being intermediate stages in the evolution of the more typical *Licuala* leaf. The striking entire leaf of *Johannesteijsmannia*, once suggested to represent a primitive leaf form (Corner, 1966), develops in a manner similar to that

of the entire-leaved species of *Licuala* and possesses the shallow induplicate lobing of the apical margins (Dransfield, 1970).

Another unusual type of splitting occurs in *Rhapis* and *Rhapidophyllum*. In these two genera, the major leaf splits occur between the folds rather than along the folds. The folds do not reach the insertion of the blade, although they may very nearly do so. These inter-fold splits usually divide the blade into segments composed of several folds; the apical margins of the segments are shallowly induplicately lobed as in *Licuala*. The inter-fold splits occur much earlier in the development of the leaf than the shallow adaxial splits of the margins.

Phoenix is the only pinnate-leaved genus in the subfamily. The leaflets are induplicate and the leaf is exceptional in its development. A broad expanse of tissue, called the "haut," on the adaxial surface of the developing leaf develops from interdigitation and proliferation of epidermal cells at the adaxial folds (Periasamy, 1967). As the sword leaf expands the haut disintegrates. There is no known parallel to the haut elsewhere in the family and its morphology and development deserve further investigation. The adaxial splits in the leaf of *Phoenix* divide the blade seemingly to the rachis, although close examination shows a thin band of lamina tissue along the rachis connecting the bases of the leaflets.

Some generalizations can be made about the different types of splits in the coryphoid leaf. Adaxial splits never reach the insertion of the blade and usually seem to occur relatively late in leaf development. We regard this type of splitting mechanism to be the simplest, and it seems to be intimately related to the mechanical forces imposed on the expanding leaf. Almost always, abaxial splits extend to the insertion on the costa or petiole. An exception is the leaf of *Guihaia*, in which the abaxial splits only reach about ½–¾ of the radius. Where the development of the abaxial splits has been investigated, they occur much earlier in leaf development than the adaxial splits, long before the mechanical forces of leaf expansion. Adaxial splits appear to be the generalized state in the Coryphoideae; abaxial splits, such as those in *Licuala*, appear to be a superimposed secondary development, a specialization. However, the deep, central, abaxial split found in *Itaya*, *Chelyocarpus*, and some species of *Cryosophila*, paralleled in Cyclanthaceae and *Curculigo seychellensis*, may be the simplest way in which a plicate leaf can split, and could be ancestral in the family.

Unlike Corner (1966), who suggested that the complex bipinnate leaf of *Caryota* represented the primitive leaf form in the family, we regard the much simpler, simply plicate leaf, divided by incomplete splits through mechanical forces of the expanding blade, to be least specialized. The forerunners of the palm leaf, we propose, were undivided and plicate. From this relatively simple model, the complex leaves of modern palms have evolved by elaboration of the midrib of the leaf into a costa or rachis, the development of different splitting mechanisms, the development of secondary plications, and the development of complex patterns of necrosis at the margins to give the highly characteristic praemorse margins of several calamoid, ceroxyloid, and arecoid palms. The simplest palm leaves are, we believe, to be found among the Coryphoideae, whether palmate or costapalmate. The earliest fossil leaves that can definitely be assigned to the palms are palmate and costapalmate forms (Daghlian, 1981). However, this may represent differential preservation or the greater ease of identifying fragments of palmate leaves than pinnate leaves (Read & Hickey, 1972).

A feature of the palmate leaf in need of further study is the hastula. Hastulae are triangular flanges occurring at the base of the blade, usually on the adaxial surface only, occasionally also on the abaxial surface. They are present in all coryphoid palmate leaves except in *Chuniophoenix* and *Nannorrhops* (Corypheae) and *Lodoicea* and *Medemia* (Borasseae). In *Johannesteijsmannia* the developing leaf bears a well defined hastula, which disintegrates just before the sword leaf emerges, leaving almost no vestige in the mature leaf. The reduplicate palmate leaves of the calamoid palms *Mauritia*, *Mauritiella*, and *Lepidocaryum* do not display clear hastulae. Hastulae are usually small, rarely more than 1 cm long, but in some Cuban members of *Copernicia* (Corypheae) they are spiny margined and greatly enlarged, sometimes over 50 cm long (e.g., in juveniles of *C. rigida* Britt. & Wils. and *C. macroglossa* H. A. Wendl. ex Becc.).

The adaptive significance of these structures is not known. They could be of mechanical significance or perhaps direct rainwater away from the apical bud. There is no doubt that the hastula directs rainwater away from the petiole and hence the palm apex (Dransfield, pers. obs. on *Livistona rotundifolia* (Lam.) Mart. in the wild), and *Medemia* and *Nannorrhops*, lacking hastulae, are plants of low-rainfall areas, but so are the species of *Copernicia* with the largest hastulae.

A. K. Irvine (pers. comm.) has recently drawn our attention to the presence of a small flange of tissue on the adaxial surface of the leaf rachis of the pinnate-leaved *Oraniopsis appendiculata* (F.

M. Bailey) J. Dransf., A. K. Irv. & N. Uhl (Ceroxyloideae: Ceroxyleae); it bears some resemblance to a hastula (Uhl & Dransfield, 1987). Subsequently we have found similar flanges in members of the closely related *Ceroxylon* and the much more distantly related pinnate-leaved *Polyandrococos pectinata* Barb. Rodr. and *Cocos nucifera* L. (Arecoideae: Cocoeae). It is tempting to suppose that this flange is homologous with a hastula, but we may only speculate on its nature until developmental work can be carried out.

Discussion

Within the palm family can be found many of the features regarded as apomorphic for and helping to define the monocotyledons: sympodial habit, leaves with sheathing bases and parallel venation, and floral parts composed of three. Some features of palms are interpreted as plesiomorphic in monocotyledons; for example, in the apocarpous palms of the Coryphoideae (Thrinacinae and Phoeniceae) the carpels are conduplicate and follicular, and have open ventral sutures, features regarded as plesiomorphic in the Angiosperms as a whole. Pollen of the least specialized modern group of palms is, for the most part, as demonstrated above, of a generalized type common in other monocotyledonous families and considered to be plesiomorphic. The most distinctive feature of the palms, the leaf, seems clearly to have been derived from an undivided but plicate form, a leaf type found scattered among the monocotyledons. The plicate leaf divided by clearly defined splits is perhaps the only reliable apomorphy for the whole family.

In the past, the palms have usually been associated with the Pandanaceae and Cyclanthaceae because of superficial similarities of habit and leaf structure respectively. Yet little, if anything, links the families in inflorescence or flower structure. Recently, in fact, the distinctness of the three families has been recognized. Thorne (1983) and Dahlgren et al. (1985) placed palms in a separate evolutionary line. With no synapomorphies clearly established to link the palms with other families, the palms remain isolated taxonomically. Perhaps current cladistic studies will clarify this (Dransfield & Uhl, in prep.).

Some authors, such as Cronquist (1981) and Muller (1984), have regarded palms as a secondary radiation from a monocotyledonous stock. Muller (1984) indeed stated that the palms did not evolve until the late Cretaceous, citing as support the appearance of supposed *Nypa* pollen in the Maestrichtian. Although the present authors do not dispute that the earliest definite fossils do not occur until the late Cretaceous, the fact that they are recognizable as palms is due to specialized features. As demonstrated here, many of the extant palms regarded as being least specialized have pollen grains of a plesiomorphic nature, indistinguishable as yet from many other monocotyledons and in fact very similar to the early Cretaceous grains illustrated by Walker & Walker (1985, 1986). It is suggested that palms probably arose before the late Cretaceous.

Palms display many evolutionary trends; while possessing characters regarded as plesiomorphic in the monocotyledons (and this seems not to be widely appreciated), they also display many specializations. It appears to the authors that palms retain characters of a very early monocotyledonous stock from which more specialized palms and, perhaps, some other monocotyledonous families may have evolved.

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POLLINATION AND THE EVOLUTION OF BREEDING SYSTEMS IN PANDANACEAE[1]

Paul Alan Cox[2]

Abstract

The Pandanaceae include three genera: *Pandanus* with 700 species and a large range, *Freycinetia* with 200 species and a smaller range, and *Sararanga* with two species and a very limited range. Using Cyclanthaceae, Araceae, and Arecaceae as outgroups, cladistic analysis of Pandanaceae suggests *Pandanus* and *Sararanga* to be more closely related to each other than either is to *Freycinetia*. Data concerning pollination biology and breeding systems are superimposed upon the consensus tree derived from this analysis. Vertebrate pollination and dioecism appear to be ancestral in Pandanaceae, with anemophily in *Pandanus* and entomophily in *Sararanga* to be independently derived conditions. Only a few changes in inflorescence morphology were necessary to facilitate these profound changes in pollination syndromes. Dioecism, while perhaps adaptive for vertebrate-pollinated Pandanaceae such as *Freycinetia*, may have been maladaptive for *Pandanus* and *Sararanga*. The ill-effects of dioecism on long-distance dispersal have been partially overcome in *Freycinetia* by the evolution of "leaky dioecy" and self-compatibility and largely overcome in *Pandanus* through the evolution of facultative apomixis. The deleterious effects of dioecism appear to be unmitigated in *Sararanga* and may lead to its eventual extinction. The interplay of pollination syndromes and breeding systems appears to have strongly influenced range expansion and speciation in the Pandanaceae.

Within the last decade or so, great interest has been directed toward the evolution of breeding systems in seed plants, particularly the evolution of different sexual systems such as monoecism, dioecism, and gynodioecism. Traditionally these systems have been considered to be disparate and distinct, providing the basis for various classification schemes such as the sexual system described by Linnaeus (Linnaeus, 1754). However, by considering a plant to be a metapopulation of modules (White, 1979), the recognition of nested modular levels in plants permits analysis of the different sexual systems at the modular level. Using this modular approach, all sexual systems can be considered merely as combinations of monomorphic or dimorphic sexual strategies (Cox, 1988) at different modular levels. Thus, for example, monoecism and dioecism can both be considered asexually dimorphic strategies occurring at the level of the shoot and the individual, respectively. Using the techniques of evolutionary game theory (Maynard Smith, 1982) as developed for sex allocation theory (Charnov, 1982) these different sexual strategies can be examined for evolutionary stability in any particular population. By definition, an evolutionary stable strategy (ESS) is one such that if all members of a population adopted it, then no individual with a different strategy could invade the population through the forces of natural selection (Maynard Smith, 1982).

The strength of the combination of game theory and a modular approach is that the effects of various ecological factors on the evolutionary stability of different breeding systems can be examined quantitatively. For example, vertebrate pollination was found to maintain dioecism as the evolutionarily stable breeding system in *Freycinetia reineckei* in Samoa (Cox, 1982). However, a weakness of this approach, and indeed one shared by all ecological approaches to evolution, is that ecological plausibility does not necessarily imply evolutionary causality.

The questions of real interest in evolutionary ecology do not merely address the factors that currently maintain a particular trait (such as dioecism), but rather seek the factors that favored the evolution of the trait. However, such determinations cannot be made effectively by an ecological analysis without due consideration of the phylogenetic relationships involved. Indeed, ecological

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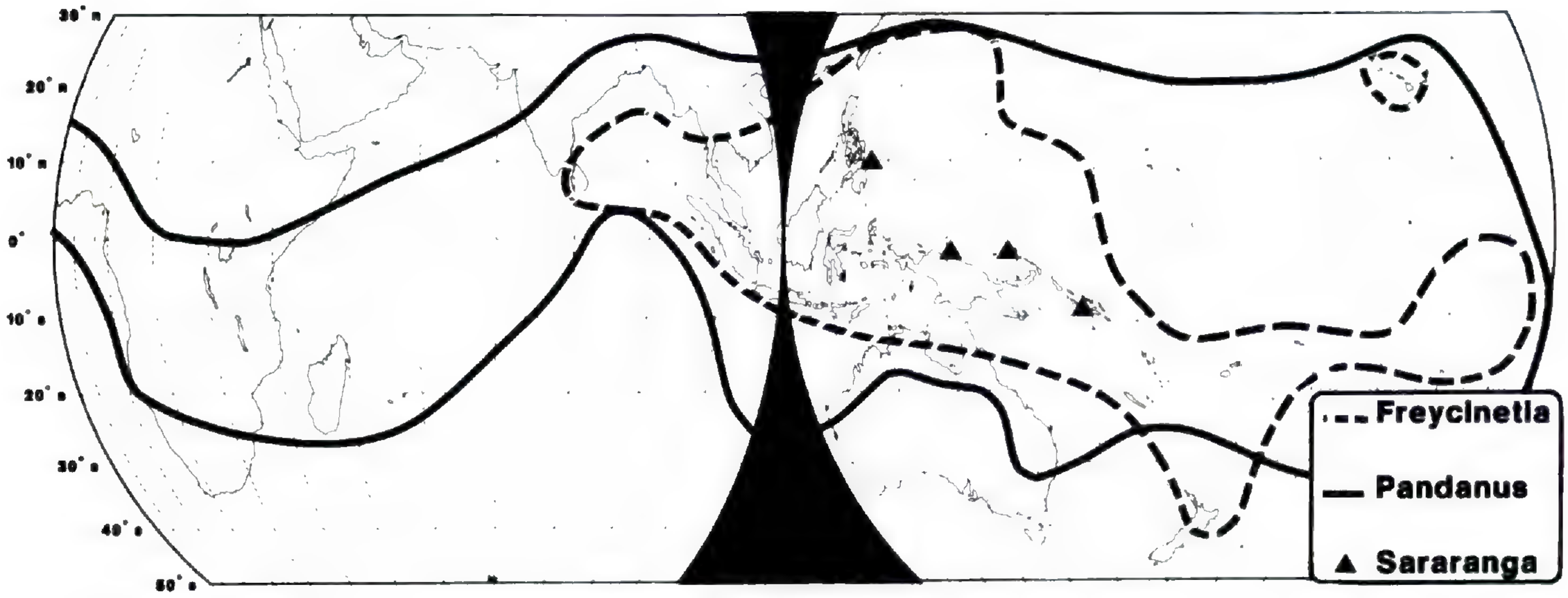


FIGURE 1. Geographical distribution of the Pandanaceae.

approaches to evolutionary questions may produce serious errors in interpretation if phylogenies are ignored.

For example, an ecological analysis of the childhood diseases of nineteenth- and twentieth-century European royalty, using the incidence of disease in commoners as a control, would indicate a significant correlation between hemophilia and access to silver drinking vessels, perhaps suggesting silver to be a causal factor in hemophilia. However, this "silver chalice fallacy" can be avoided by examining the genealogy of the group, which clearly indicates that hemophilia among European royalty is inherited from a single autosomal mutation in Queen Victoria.

Cognizance of phylogenetic constraints can also give an indication of characters that are unlikely to have evolved in a particular lineage. Androdioecism is very unlikely to have evolved in any of the ancestors of, for example, *Scaevola taccada* (Goodeniaceae), since phylogenetic analysis shows that all of *Scaevola* and indeed nearly all of the Goodeniaceae have anthers that dehisce and wither in bud, with pollen being presented by the pendulous, indusiate stigma. Thus, it would be very difficult for a male to disperse its pollen in the absence of a morphologically complete gynoecium.

Therefore when examining breeding system evolution in the Pandanaceae, to avoid some of the pitfalls inherent in plausibility arguments based solely on ecological considerations, it is advantageous to determine first the phylogenetic history of the group. Once a phylogenetic hypothesis, in this case represented as a cladogram, is determined with some degree of confidence, various trends of evolution of the breeding system within the group can be analyzed within this systematic context. Note, though, that the resultant analysis should be considered only as a hypothesis, since its validity ultimately rests upon the putative phylogeny, which may change as more information becomes available.

Systematic Relationships in Pandanaceae

The Pandanaceae, the sole representatives of the Pandanales, are arboreous or scandent monocotyledons confined to the Old World tropics and subtropics (Fig. 1). The family consists of three genera. *Pandanus* is made up of approximately 700 species of trees ranging from the Society Islands to west Africa on an east-west axis and from Australia to the foothills of the Himalayas on a north-south axis (St. John, 1965; Stone, 1976b). *Freycinetia* is a genus of about 180–200 species of lianas ranging from the Society Islands to Sri Lanka on an east-west axis, and from New Zealand to the Himalayas on a north-south axis. *Sararanga* comprises two arboreous species: *S. philippinensis* from the Philippines, of which few recent collections exist; and *S. sinuosa*, which is found along the edge of the Tethys geosyncline in the Solomons, Admiralties, and North Irian Jaya.

The Pandanaceae are very distinctive and disjunct monocotyledons and likely are a group of great antiquity: *Pandanus* pollen has been described from the late Cretaceous and early Tertiary (Jarzen, 1978; Muller, 1981) while at least one megafossil from the early Eocene has been attributed to the family (Nambudiri & Tidwell, 1978; Bande & Awarthi, 1986).

Systematic studies of the Pandanaceae have been made by several investigators including Warburg (1900), Martelli (1934), Merrill & Perry (1939), and most recently St. John (1960, and elsewhere),

Stone (1968a, and elsewhere), and Huynh (1980). The revision of *Pandanus* by St. John (1960, and elsewhere) is now in its 47th part, and the monograph of *Freycinetia* by Stone (1967, and elsewhere) will soon be completed. However, even though Pandanaceae appear to represent a monophyletic group, the relationship of Pandanaceae to other families of monocotyledons remains poorly understood. Conjecture regarding the systematic relationships of the family ranges from the view that Pandanaceae are very primitive monocotyledons to the view that they are very advanced. Meeuse (1965, 1966) suggested the Pandanaceae are relict representatives of the fossil order Pentoxylales, while Engler & Gilg (1924) regarded it as the most primitive monocotyledonous family with affinities to the Typhales (a view shared by Rendle, 1904, and Takhtajan, 1980). However, Stone (1972a) and Cronquist (1968) suggested affinities with Aracaceae and Cyclanthaceae, a view which has been supported recently through phenetic analysis by Dahlgren & Clifford (1982) and in a cladistic revision by Dahlgren & Rasmussen (1983). However, the precise relationship of Pandanaceae to other families of monocotyledons remains undetermined as even its sister group has yet to be demonstrated convincingly.

Relationships among the genera of Pandanaceae are similarly unclear even though these three genera are quite distinct; as Stone (1972a) pointed out, there are no "freycinetoid" *Pandanus* species and no "pandanoid" *Freycinetia* species. Stone suggested that *Freycinetia* is the most "specialized" genus but "somewhat more distant from the other two genera than the latter two are from each other" (Stone, 1972a, p. 40). Stone believed *Sararanga* possesses the greatest number of primitive characters. In a similar vein, Dahlgren et al. (1985) argued that "*Sararanga* is more ancestral in its floral construction than either of the other genera."

Stone's (1972a, 1982a) view of the relationships among the three genera, with *Sararanga* and *Pandanus* being more closely related to each other than either is to *Freycinetia*, is supported by my preliminary cladistic analysis of generic relationships within the family. Three major difficulties were encountered in this analysis at the generic level. First and foremost among these is lack of a clear sister group to Pandanaceae, although Araceae, Arecaceae, or Cyclanthaceae are all potential outgroups (Harling, 1958; Dahlgren & Clifford, 1982; Dahlgren & Rasmussen, 1983; Dahlgren et al., 1985). Second, the taxonomic status of these potential outgroups is unclear. If, for example, the Cyclanthaceae prove not to be monophyletic, their use as a single outgroup in a cladistic analysis would be invalid. Third, the distinctiveness of the family makes it difficult to find a large number of characters that vary at the generic level within the Pandanaceae but remain constant at the familial level in the outgroups. This would not be a problem if in-group analysis had been done within these other families, but such analyses are far beyond the scope of this paper.

To overcome these problems, the potential outgroups Araceae, Arecaceae, and Cyclanthaceae were represented by single genera. These genera—*Rhaphidophora* (Araceae), *Balaka* (Arecaceae), and *Asplundia* (Cyclanthaceae)—were chosen solely on the basis of my familiarity with them in the field, although in the case of *Asplundia* my observations were checked against Harling's (1958) monograph of the Cyclanthaceae. Fourteen different character states were scored for these outgroup genera and the three genera of the Pandanaceae. Using this data matrix (Table 1), the most parsimonious cladogram for the Pandanaceae was determined for each outgroup. All three of these trees, however, were found to have the same general topology (Figs. 2–4), which indicates that *Pandanus* and *Sararanga* are more closely related to each other than either is to *Freycinetia*. This result is believed to be relatively robust since the general topology remains unchanged even when the entire Cyclanthaceae, Araceae, and Arecaceae are used instead of their representative genera as outgroups, although the character number is reduced. From these three different phylogenetic trees, a consensus tree (Fig. 5) can be drawn that shows features common to the other trees. As a caveat it should be noted, however, that despite the tremendous efforts of workers such as Stone and St. John, Pandanaceae in general remain poorly collected and insufficiently studied, and hence this preliminary analysis of generic relationships is subject to revision as data accumulate. Monophyly of the genera, for example, should be rigorously demonstrated rather than assumed as I have done here. The current analysis is intended as a method of generating hypotheses concerning evolution of plant breeding systems and as a means of pointing out areas where more information is required.

In the consensus tree (Fig. 5) Pandanaceae are characterized by three synapomorphies, namely spiny leaf margins, dioecism, and tristichous phyllotaxy (characters 12, 13, and 14, respectively). A fourth character, clustering of ovaries into syncarps, is a probable synapomorphy for the family but was not used in this analysis since many apparent reversals occur, such as sections *Acrostig-*

TABLE 1. Character states in Pandanaceae.

Numbers	Character transition (old to new)	*Freycinetia*	*Pandanus*	*Sararanga*	*Balaka*	*Raphidophora*	*Asplundia*
1.	Numerous ovules to solitary ovule	0	1	1	0	0	0
2.	Parietal placentation to other placentation type	0	1	1	1	0	0
3.	Seeds unprotected by seedcoat to thick, or endocarp thick	0	1	0	0	0	0
4.	Spikes arranged in pseudoumbellate involucre to spikes otherwise disposed	1	0	0	0	0	0
5.	Inflorescence bracts not fleshy to inflorescence fleshy	1	0	0	0	0	0
6.	Inflorescence spicate to inflorescence paniculate	0	0	1	1	0	0
7.	Primary phyllotaxis maintained to secondary torsion causing pseudospiral leaf arrangement	0	1	1	0	0	0
8.	Phyllotaxis same in juvenile and adult to phyllotaxis changes with maturity	0	0	1	0	0	0
9.	Leaves with sheathing base or auricle to leaves without sheathing base or auricle	0	1	1	0	0	0
10.	Aerial roots present to aerial roots not present	0	0	1	1	0	0
11.	Scandent habit to arboreous habit	0	1	1	1	0	0
12.	No spines on leaf margins to spines on leaf margins	1	1	1	0	0	0
13.	Breeding system various to breeding system dioecious	1	1	1	0	0	0
14.	Phyllotaxis various to phyllotaxis tristichous	1	1	1	0	0	0
15.	Tepal primordia present to tepal primordia absent	0	1	1	0	0	0

ma, *Jeanneretia*, *Bryantia*, *Curviflora*, *Maysops*, and *Cauliflora* of *Pandanus*, which have single-celled drupes that are not connate into phalanges (Stone, 1972b). The belief that these cases illustrate reversals from ancestral forms with compound ovaries must remain an assumption until a cladogram for internal relations of genera and subgenera within Pandanaceae is developed.

Major characters of systematic importance within the family include ovule number (character 1), placentation (character 2), and secondary torsion in the phyllotactic arrangement (character 7). *Pandanus* and *Sararanga* are characterized by solitary ovules, absence of tepal primordia during floral organogenesis, and leaves without sheaths or auricles at the base. However, *Pandanus freycinetioides* and *P. parvus* exhibit rare or occasional multiple ovules (though few—only two or three) (Cheah & Stone, 1975). The evidence for tepal primordia is based on only a few examples out of some 800 species. In *Pandanus* and *Sararanga* juvenile (i.e., prereproductive) axes, the initial tristichous arrangement of the leaves is obscured by secondary torsion of the axis, creating a pseudospiral leaf arrangement (Figs. 13c, 15c). The sister group to *Pandanus* and *Sararanga*, *Freycinetia*, is characterized by numerous ovules, the presence of tepal primordia during floral organogenesis (Fig. 8b), no secondary torsion in the tristichous phyllotaxis, and auricles at the leaf bases. The systematic usefulness of the last-mentioned character at an intergeneric level may be subject to revision, however, as studies of leaf organogenesis in all three genera of Pandanaceae and in the probable outgroups are necessary to test whether auricles and leaf sheaths have a similar ontogeny and are indeed homologous. Such an ontogenetic analysis is important since the leaf bases in *Pandanus* sect. *Jeanneretia* and sect. *Dauphinensia* have auriclelike sheaths almost as distinct as in *Freycinetia*, though they are not caducous.

Two autapomorphies (characters 4, 5) characterize *Freycinetia* in all three trees: fleshy bracts (Fig. 6c) and telescoping of the inflorescence, which results in a pseudoumbellate involucre. The role of both features in pollination will be discussed later. There is an additional possible autapormophy, viz. epidermal-cell papillae on filaments of stamens (Stone, 1971).

A single autapormophy, i.e., seeds protected by a hard endocarp (character 3), characterizes *Pandanus* in the consensus tree.

Sararanga is characterized by a single autapomorphy common in the consensus tree: an onto-

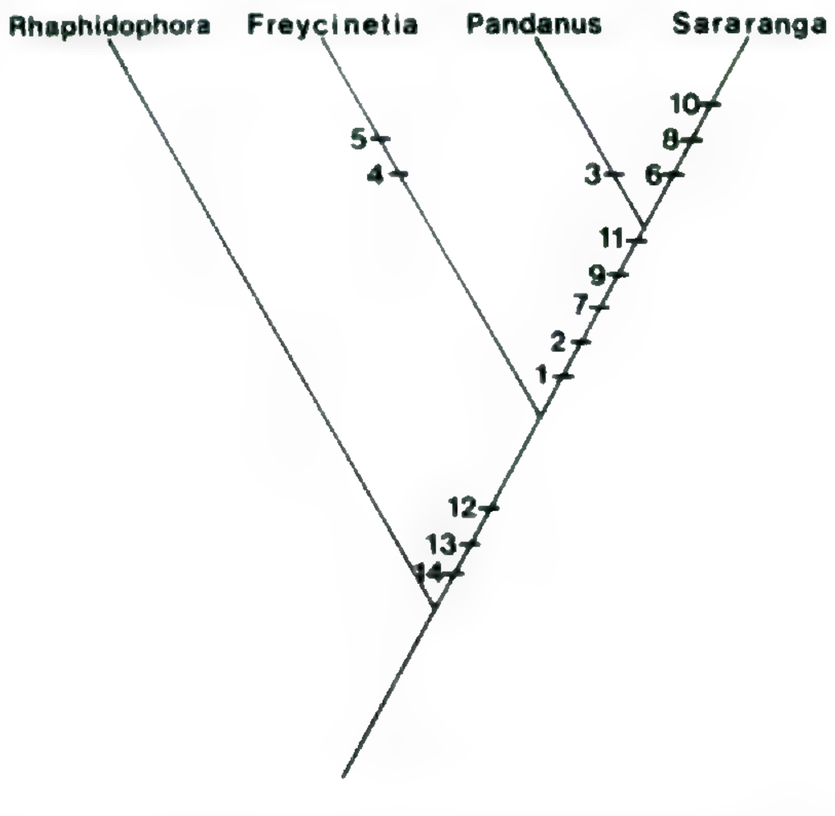


FIGURE 2. Most parsimonious cladogram of the Pandanaceae using the characters in Table 1 and using *Rhaphidophora* (Araceae) as the outgroup.

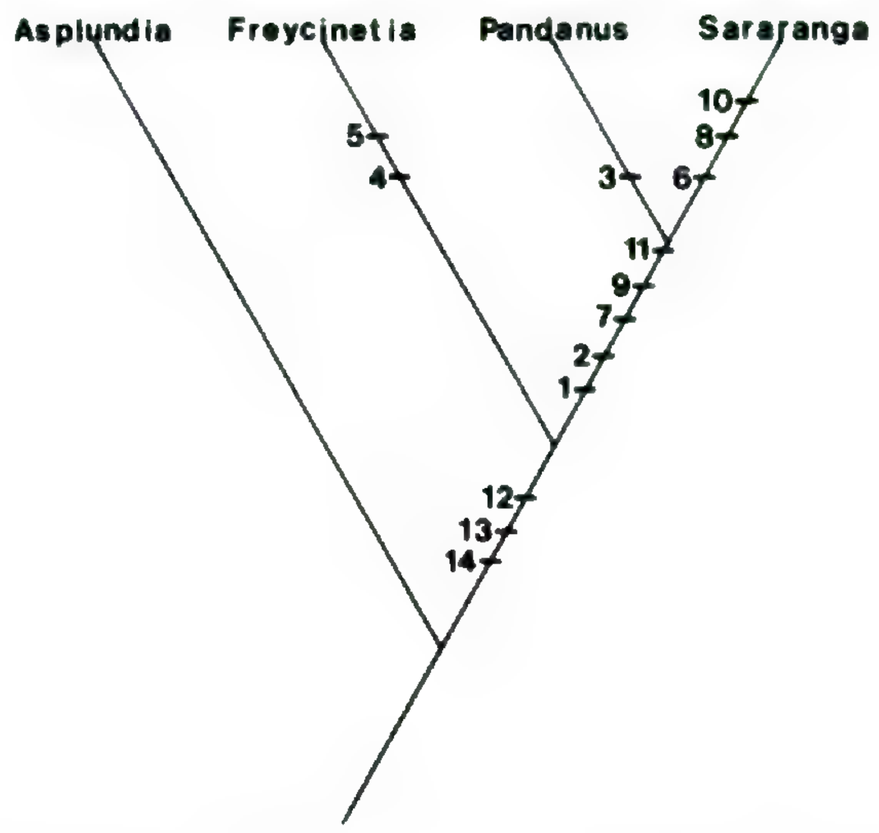


FIGURE 4. Most parsimonious cladogram of the Pandanaceae using the characters in Table 1 and using *Asplundia* (Cyclanthaceae) as the outgroup.

genetic change in phyllotaxis (character 8). Since this change has not previously been noted it merits brief discussion here.

In *Sararanga sinuosa* Hemsl. populations in Guadalcanal (Fig. 7), Tulagi Island (Fig. 8), and along the Siota Passage dividing big and little Ngela islands, I noticed a distinct difference in phyllotaxis in axes produced before and after flowering. The seedling and juvenile axis (Figs. 9, 10, 11) is always tristichous, in this respect resembling the phyllotaxis of *Pandanus* and *Freycinetia* juvenile and adult axes. As this orthotropic axis develops, a secondary torsion results in a pseudospiral leaf arrangement similar to the adult and juvenile axes of *Pandanus*.

The tristichous axis of *Sararanga* continues growth without branching to a height of approximately 6–10 m when it is terminated by an inflorescence (Figs. 7c, 10c, 10d). Three buds in the axils of leaves beneath this inflorescence continue growth, but these axes and all subsequent axes appear to be tetrastichous, with their leaves in four rather than three ranks, and lack any secondary torsion of the axis (Figs. 10, 11). The precise nature of the phyllotactic arrangement in these secondary axes can be determined by measuring the length of very young leaves using a method developed by Don Kaplan (pers. comm.). For this purpose, buds of primary and secondary axes of *Sararanga sinuosa* Hemsl. collected in Tulagi and Guadalcanal were dissected from the axes in the field and then pickled in FAA (Fig. 11). These buds were subsequently sectioned serially. Each section was examined for the first or last appearances of a leaf. Thus the length of each leaf could be found by multiplying the number of sections it occurs in by the section thickness (in this case 5 μm). This

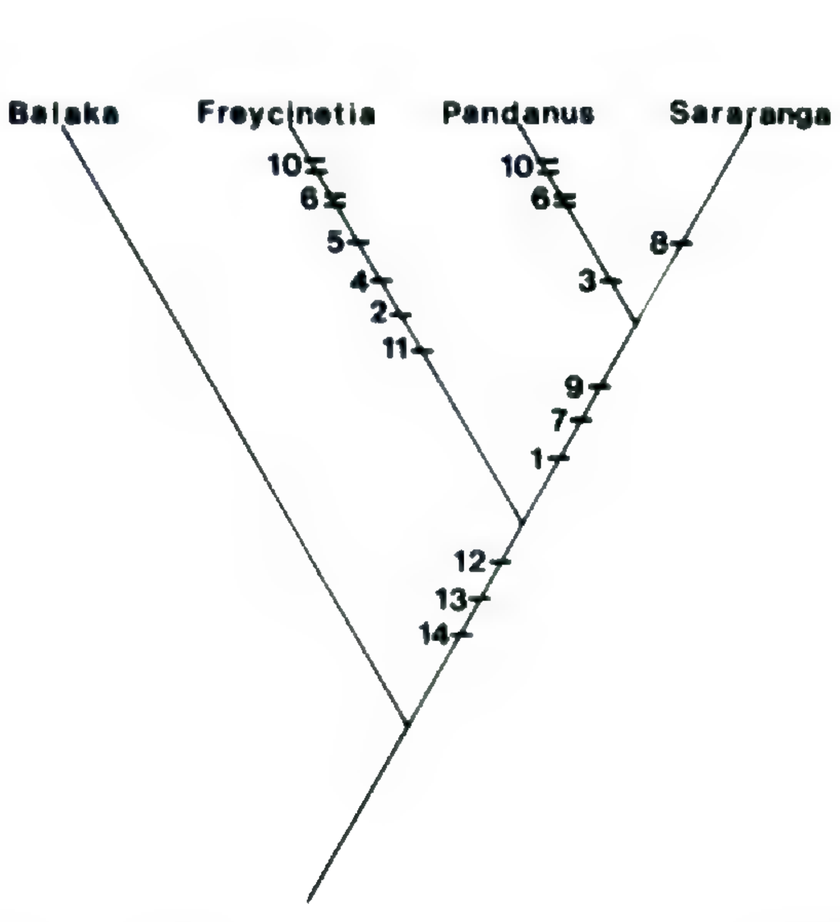


FIGURE 3. Most parsimonious cladogram of the Pandanaceae using the characters in Table 1 and using *Balaka* (Arecaceae) as the outgroup.

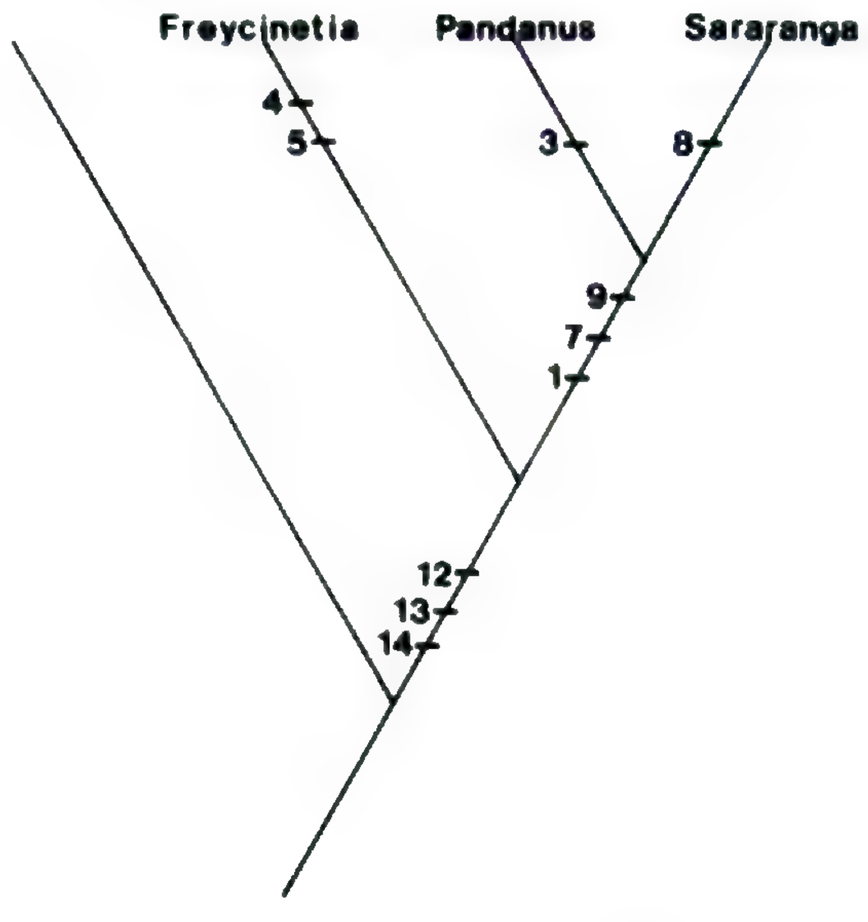


FIGURE 5. Consensus cladogram of the Pandanaceae using cladograms shown in Figures 2–4. Only character polarities common to all three cladograms are shown.

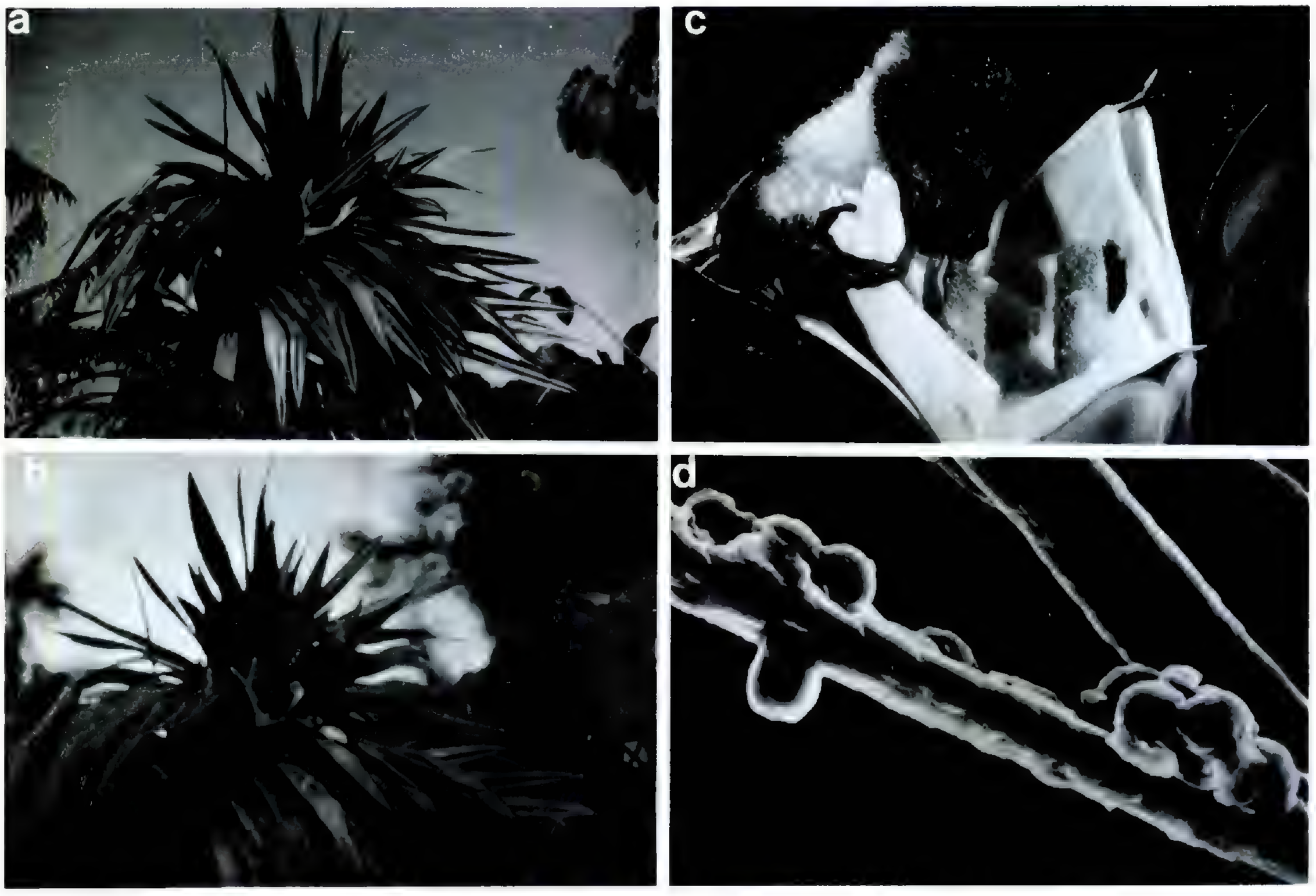


FIGURE 6. Pollination biology of *Freycinetia reineckei*.—a. Habit.—b. Pollination by *Aplonis artifuscus* (Sturnidae) in Samoa.—c. Pollination by *Pteropus marianensis* (Pteropidae) in Guam (photo by Merlin Tuttle, Bat Conservation International).—d. Pollen on facial hairs of *Pteropus samoensis* (Pteropidae) in Samoa. (Figures used with permission from J. Lovett Doust & L. Lovett Doust (editors), Plant Reproductive Ecology: Strategies and Patterns. Oxford Univ. Press, Oxford.)

analysis revealed that the apparent tetrastichy of mature (postreproductive) *Sararanga* axes results from a distichous leaf arrangement with each successive node producing a pair of opposite leaves in a plane orthogonal to the plane of the leaf pair produced by the previous node. This arrangement is obscured by the highly compressed internodes except in the inflorescence axis where the internode length is increased, and the distichous phyllotaxis is apparent.

REPRODUCTIVE BIOLOGY IN PANDANACEAE

FREYCINETIA

Floral biology. Freycinetia inflorescences are borne on hapaxanthic axes, either terminating the major axis of the liana (*F. reineckei, F. marginata*) with renewal growth occurring from an axillary bud beneath the inflorescence, or terminating axillary shoots (*F. arborea, F. scandens*). In some species the shoots arise on defoliate branches (*F. funicularis*). The pattern of serial changes in leaf form and size along the *Freycinetia* axis is similar to the pattern found in other monocotyledons (Kaplan, 1973), although the reduction in bract size toward the distal end of the axis is strikingly different from some Cyclanthaceae (Harling, 1958). The changes in leaf length, basal width, and the occurrence of marginal spines along a vegetative axis are illustrated in Figure 12. There is an increase in leaf length from the oldest leaf, the prophyll (leaf number 34) to the mature foliage leaves (leaf number 16) and thence a decrease in length to the youngest leaf (number 1), which encloses the meristem. If the axis terminates in an inflorescence, there is a distinct decrease in length and number of marginal spines toward the distal end (Fig. 12) with a smooth transition from foliage leaves to the fleshy bracts. Frequently foliage leaves immediately beneath the inflorescence have a patch of bright coloration at their base, which undoubtedly adds to the attractiveness of the inflorescence to potential pollinators. For an illustrated example of these transitions see Stone (1967).

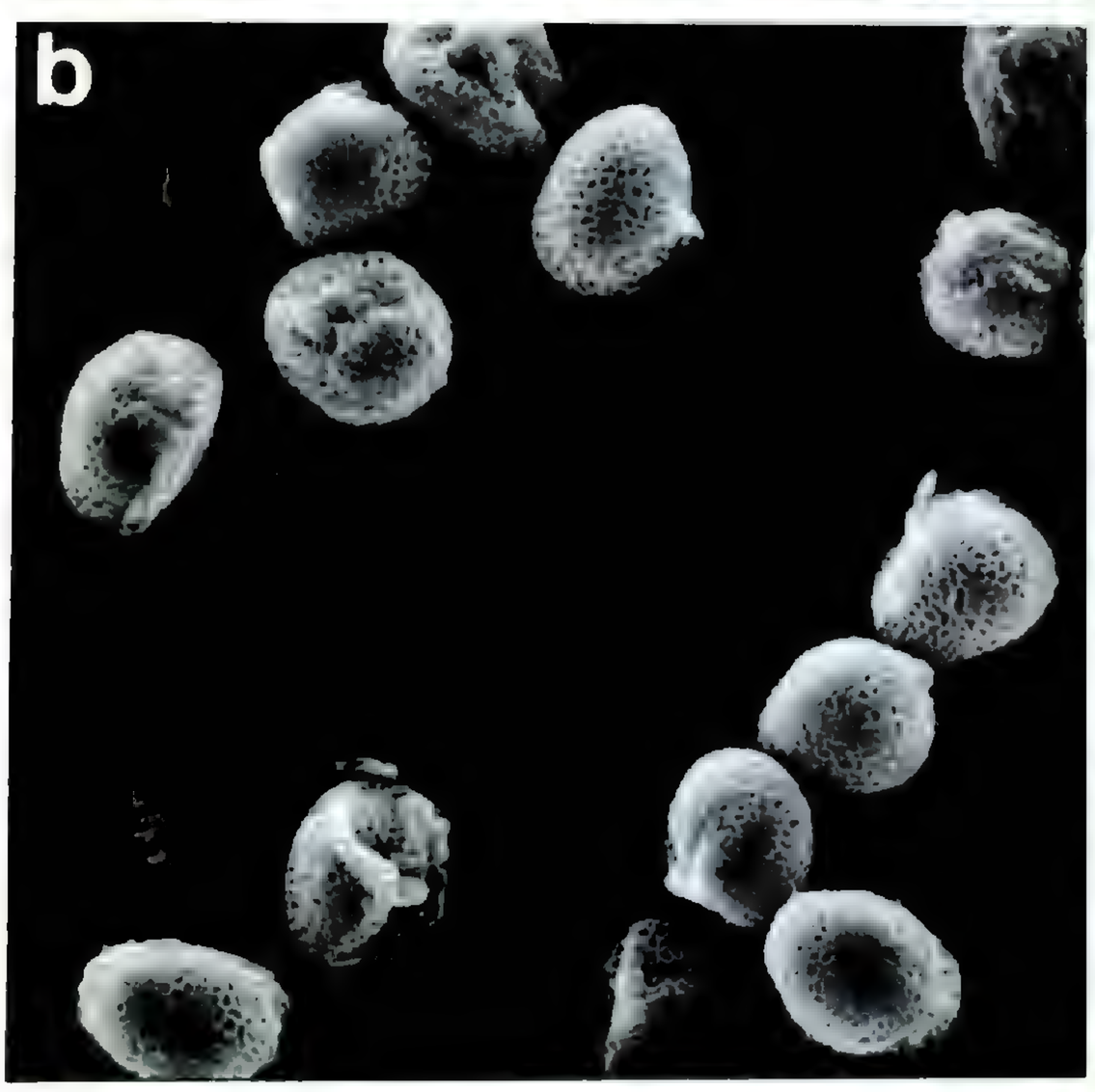
In *Freycinetia angustifolia* and *F. jagorii* the inflorescence is clearly racemose. In all or most

a

c

b

d



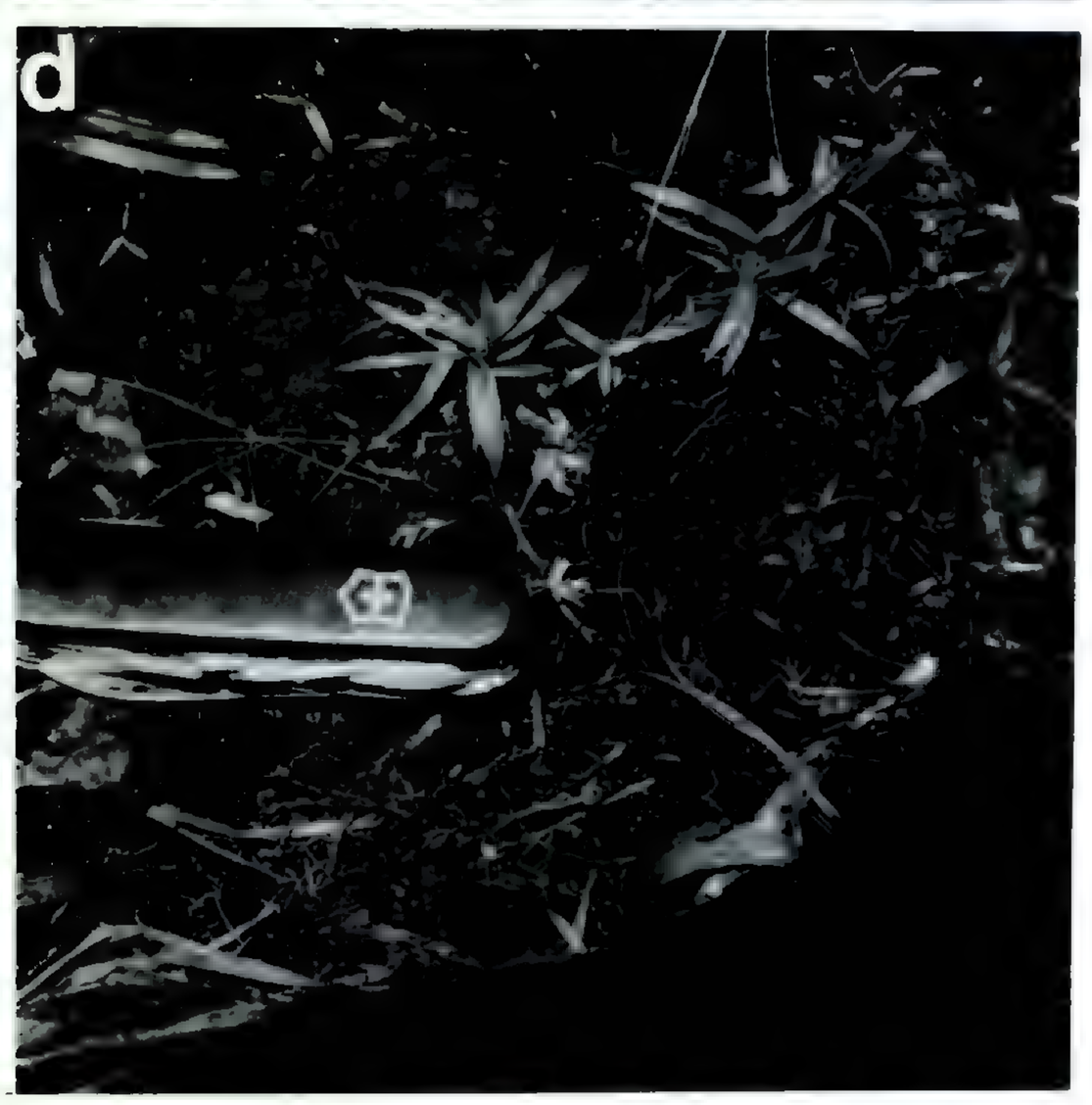


FIGURE 8. *Sararanga sinuosa* in the Solomon Islands.—a. Pendulous pistillate inflorescence in Tulagi.—b. Pollen.—c. Juvenile in Tulagi showing tristichous phyllotaxis.—d. Seedlings in Tulagi showing tristichous phyllotaxis.

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FIGURE 7. *Sararanga sinuosa* in the Solomon Islands.—a. Habit in Guadalcanal.—b. Root system in Tulagi; note absence of stilt roots.—c. Pistillate infructescence in Guadalcanal.—d. Cephalia in Guadalcanal.

FIGURE 9. *Sararanga sinuosa* in Guadalcanal, Solomon Islands.—a. Juvenile.—b. Field dissection of "a" showing tristichous phyllotaxis.—c. Larger juvenile.—d. Field dissection of "c" showing tristichous phyllotaxis.

other species, the inflorescence is a false umbel of spikes with the subtending fleshy bracts telescoped by a reduction of internode length yielding the pseudoumbellate structure. Various colors are found in *Freycinetia* inflorescences. Some species have white bracts (*F. hombronii*, *F. scandens*), while others have colored inflorescences ranging fom pale salmon (*F. arborea*) to bright reddish orange (*F. reineckei*, *F. marginata*) (Cox, 1984; Cox et al., 1984; Stone, 1982b). Some species have bright yellow bracts (*F. biloba*), while others have very dark purple bracts (*F. negrosensis*). Species with

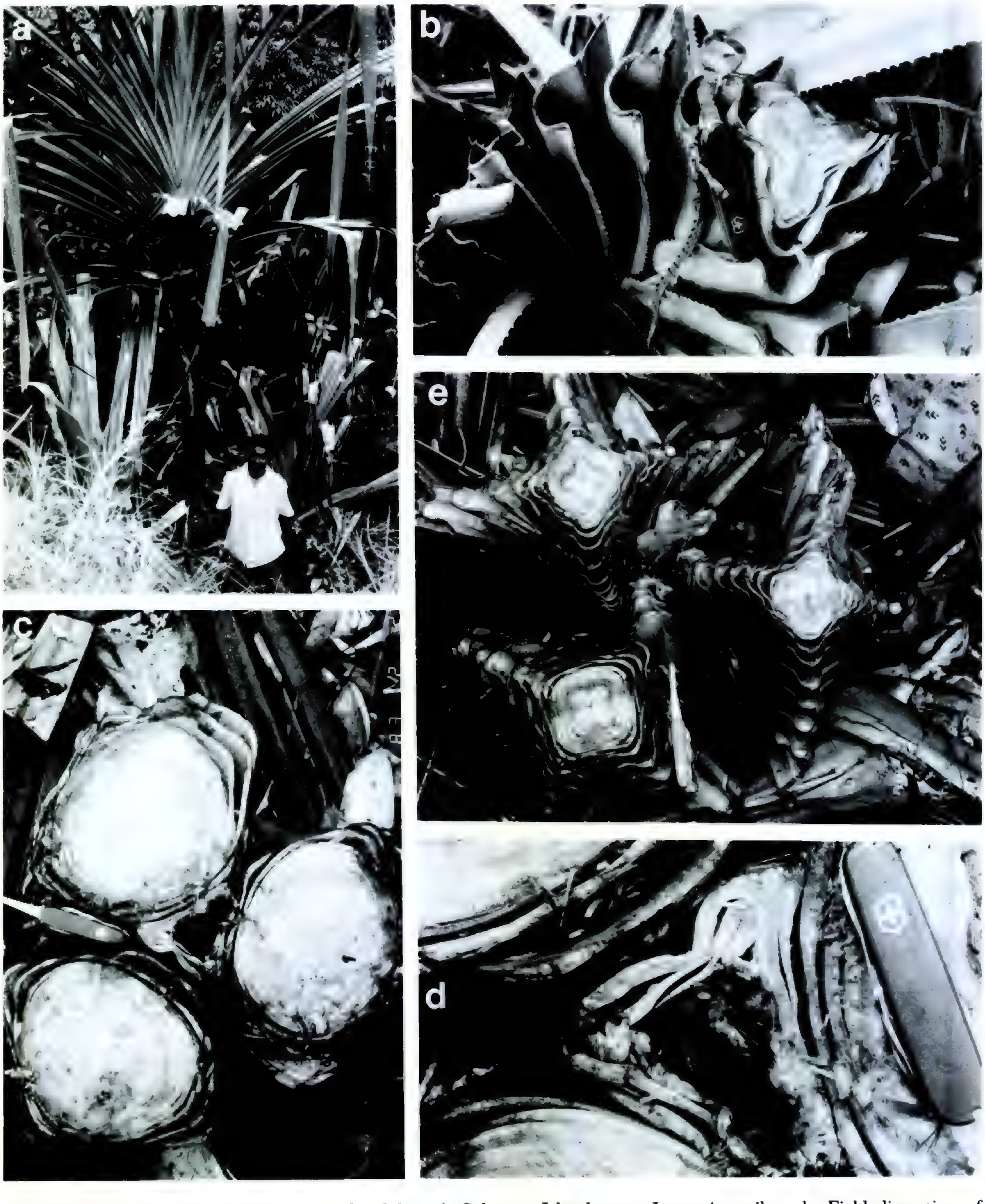
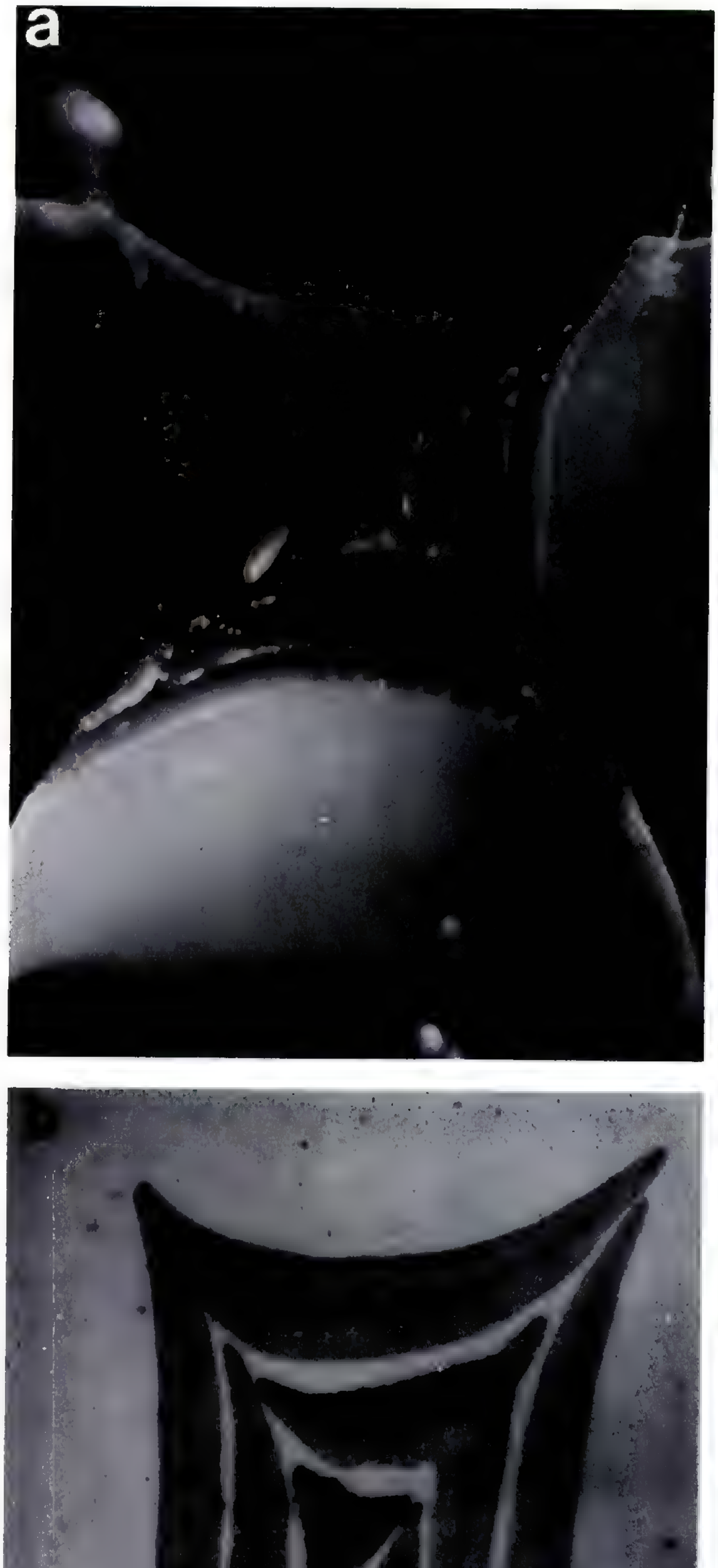
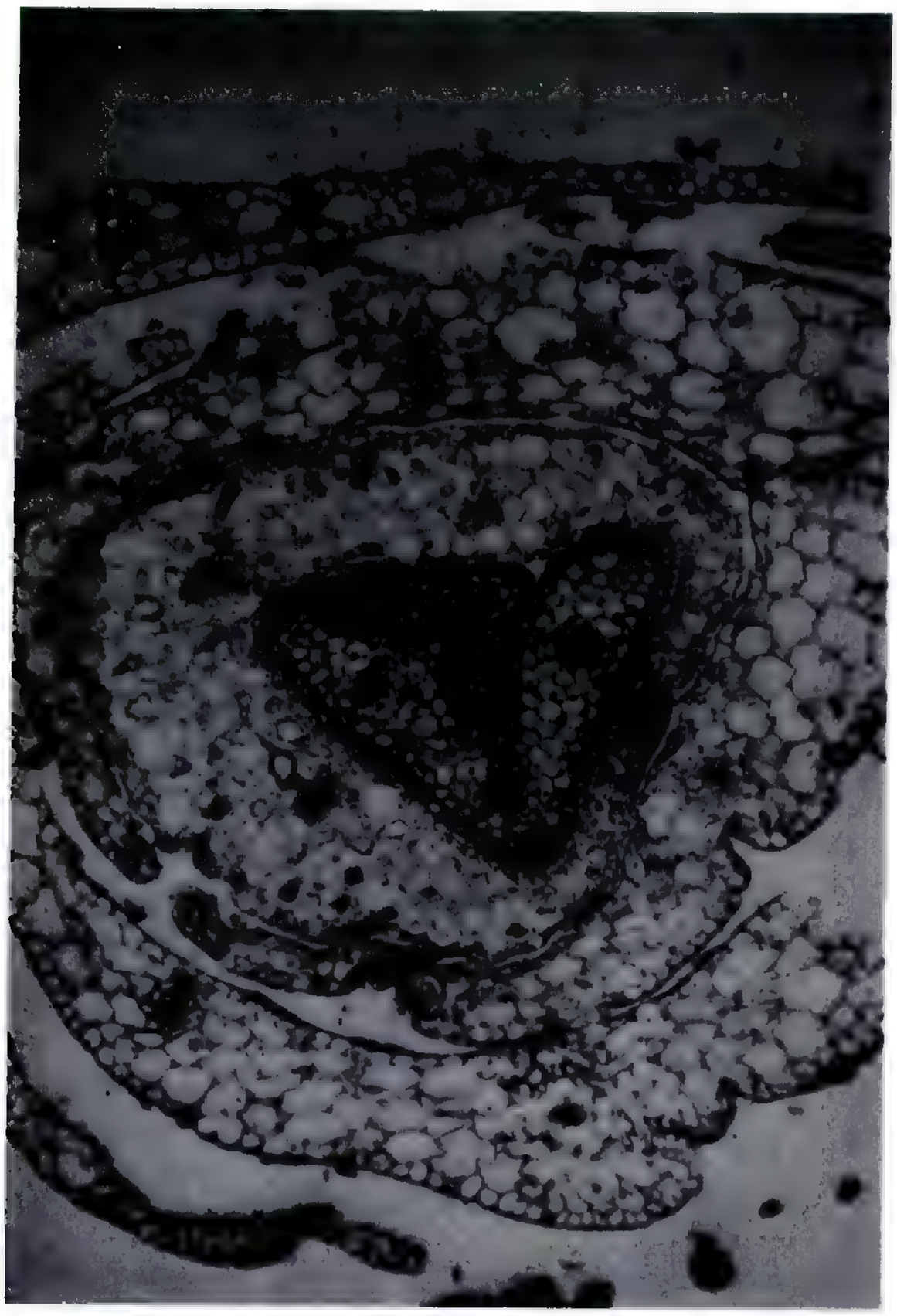


FIGURE 10. *Sararanga sinuosa* in Guadalcanal, Solomon Islands.—a. Large juvenile.—b. Field dissection of "a" showing tristichous phyllotaxis.—c. Field dissection of postreproductive individual, showing tristichous base of inflorescence and three axillary branches produced beneath inflorescence.—d. Close-up of tristichous inflorescence base.—e. Same three branches photographed prior to dissection stage shown in "c"; note superficial tetrastichy of branches.

white inflorescences produce a fetid, musky smell while those with colored inflorescences frequently lack a distinctive smell; however, this topic lacks substantive data as yet.

No liquid nectar is produced by *Freycinetia* species. Instead, the bracts themselves function as hexose-rich "solid nectar," containing up to 29% by dry weight total sugar (Cox, 1983) with particularly high concentrations of fructose (Cox, 1983, 1984; Cox et al., 1984). The bracts are also rich





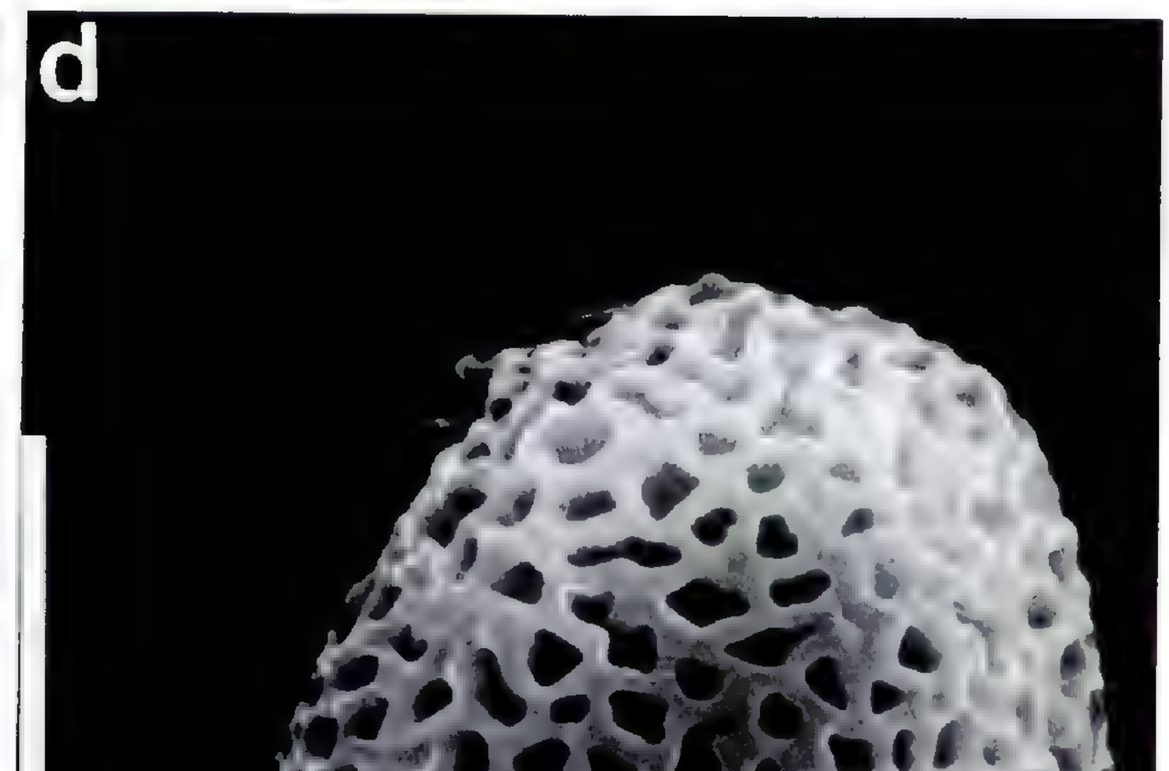


FIGURE 11. *Sararanga sinuosa*.—a. Superficially tetrastichous apex of branch produced subsequent to first flowering.—b. Cross section of "a" showing distichous nature of phyllotaxis.—c. Cross section of tristichous apex of prereproductive primary axis showing tristichous phyllotaxis.—d. Pollen with reticulate exine.

in free amino acids, with up to 9% by dry weight total amino acids (Cox, 1983), and up to 12 different amino acids present (Cox, 1984).

The number of spikes in an inflorescence usually varies between three and seven, while in *F. celebica*, the spike is usually solitary. Since each of these spikes is subtended by a fleshy bract, the shortening of internodes in this region of the axis permits the clustering of the spikes and bracts into a single anthecological unit that seems well adapted for vertebrate pollination (Fig. 6). The staminate spikes are often the same color as the distal bracts. The pistillate spikes, however, are usually green, though they may be white or pink in some species. The staminate spikes represent a high-quality reward for pollinators, as they may provide up to 26% dry weight crude protein and up to 24% dry weight lipid (Cox, 1984). Their high lipid content probably results in large part from the lipid-rich *pollenkitt* that covers the pollen.

At the terminus of the axis are several fleshy bracts (Bekonstigungskörper) that do not subtend spikes and that differ from outer bracts by being smaller and cylindrical, and by lacking marginal teeth on their tips.

The true flowers are extremely tiny and are congested on the spikes. The absence of perianth members at maturity makes delimitation of each flower very difficult, though their individuality can be discerned by studies of floral organogenesis.

Experimental. Developmental stages of *Freycinetia arborea* inflorescences were collected on the islands of Kauai and Hawaii and preserved in FAA. The spikes were bisected longitudinally. Half of each spike was stained in acid fuchsin, de-differentiated in 75% ethanol, and studied using the epi-illumination techniques of Sattler (1968). The other half was critical-point dried, coated with a silver-gold-palladium amalgam, and studied using the scanning electron microscope techniques of Uhl & Moore (1980).

With both techniques, floral units, each of which is subtended by a tiny bract (Fig. 13a), can be distinguished along the inflorescence. The outer whorl usually consists of six perianth primordia, inside of which is the whorl of androecial primordia (indicating six stamens). At a later stage of development (Fig. 13b), several gynoecial primordia develop inside the androecial whorl. In staminate spikes, however, the floral bracts, perianth, and gynoecium soon cease development (Fig. 13c) and only the androecial primordia continue developing, with the aborted gynoecial primordia forming a ring-shaped pistillode (Fig. 13d). Comparable developmental information for pistillate spikes is unavailable because the appropriate stages have yet to be collected; however, a similar sequence of events probably occurs since the mature gynoecia of many *Freycinetia* species are surrounded by numerous diminutive staminodia (Fig. 14).

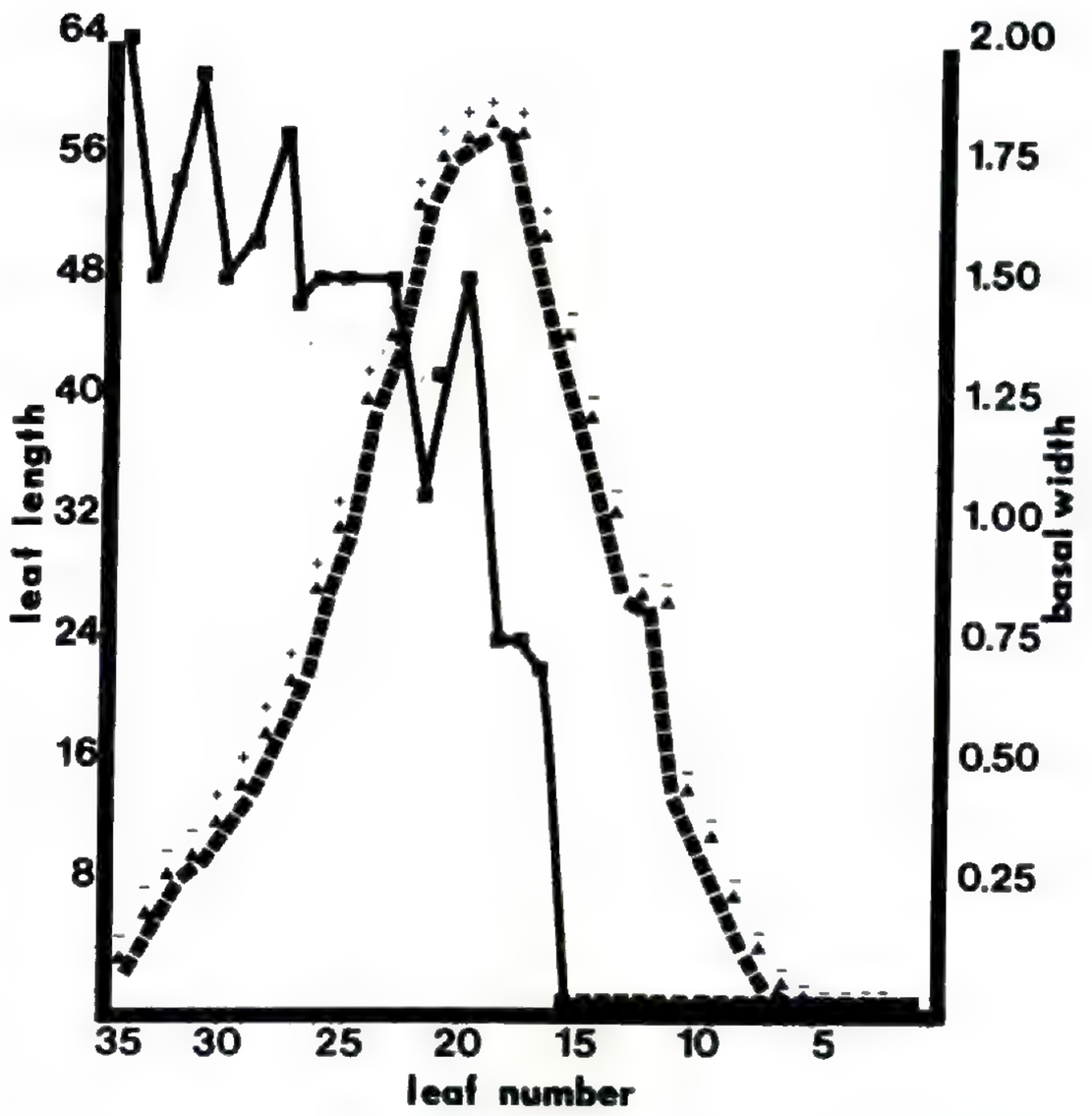
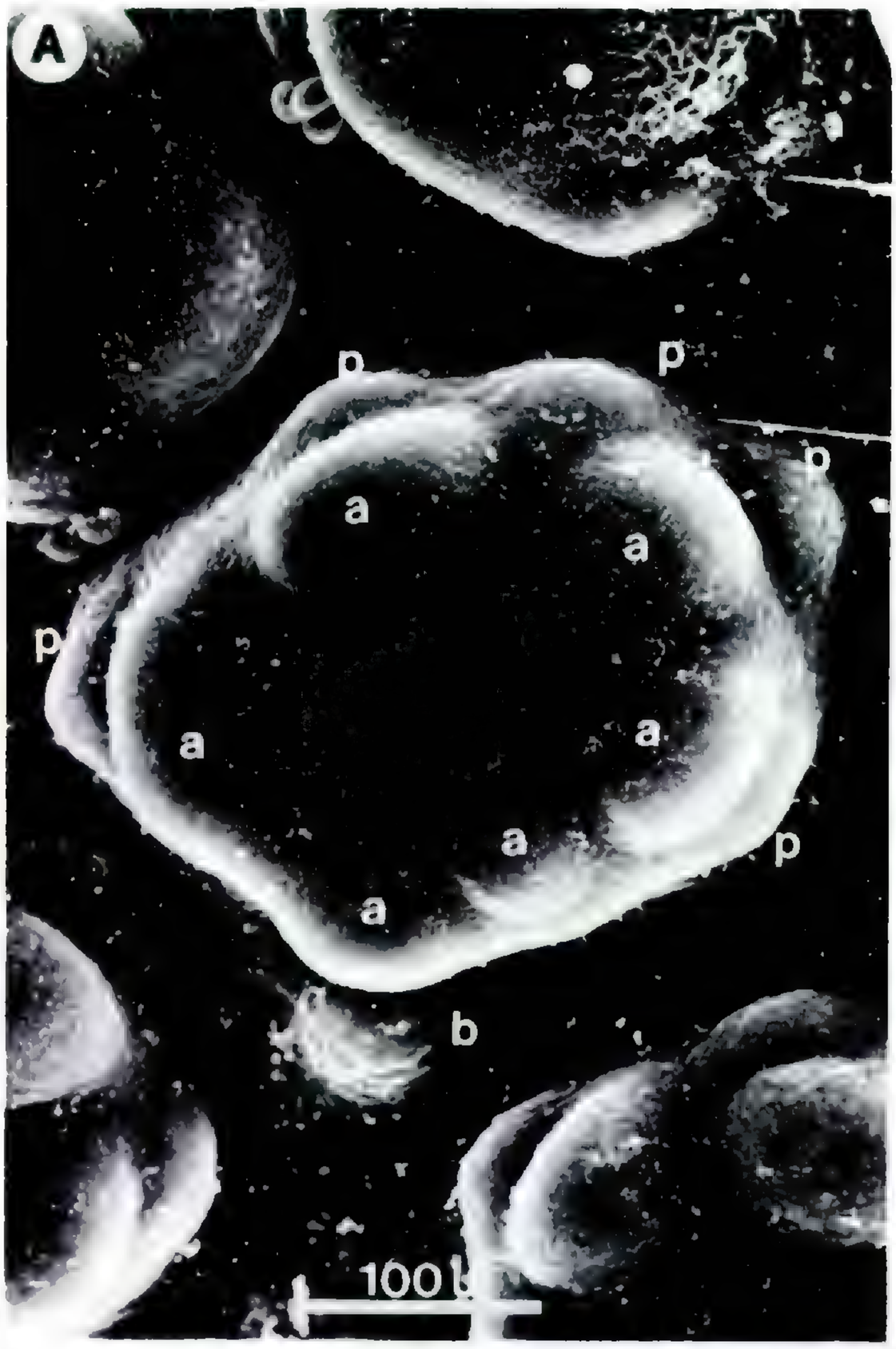


FIGURE 12. Leaves of transition along a vegetative axis of *Freycinetia reineckei*. Dotted line indicates leaf length in centimeters; solid line indicates basal width in centimeters; + or − indicates presence vs. absence of marginal spines. Leaf 34 is the prophyll, with leaves 34–16 being mature; data on leaves 16–1 (the youngest leaf) were obtained by dissection of the apical bud.

Breeding systems. Although *Freycinetia* and all Pandanaceae have been believed to be strictly dioecious (Hutchinson, 1973; Dahlgren et al., 1985), recent fieldwork has indicated that a variety of breeding systems exists in *Freycinetia* (Cox, 1981; Cox et al., 1984; Poppendieck, 1987). To discuss this diversity and its evolutionary significance, it is useful to consider a *Freycinetia* individual as a metapopulation (White, 1979) of modules. More precisely, a *Freycinetia* (or any other) plant can be viewed as having modularity at different levels, thus being composed of a nested set of modular units (Cox, 1988). In all known species of *Freycinetia* a minimum of four levels of modular construction can be recognized. For example, entire genetic individuals (Fig. 15a) of *F. reineckei* may be considered as modules at one level (let us call this level 1), and these modules could theoretically be either sexually monomorphic (all hermaphroditic) or dimorphic (pistillate and staminate). A second modular level (level 2) consists of hapaxanthic axes terminated by an inflorescence (Fig. 15b); again, these hapaxanthic axes can be sexually monomorphic or dimorphic. A third modular level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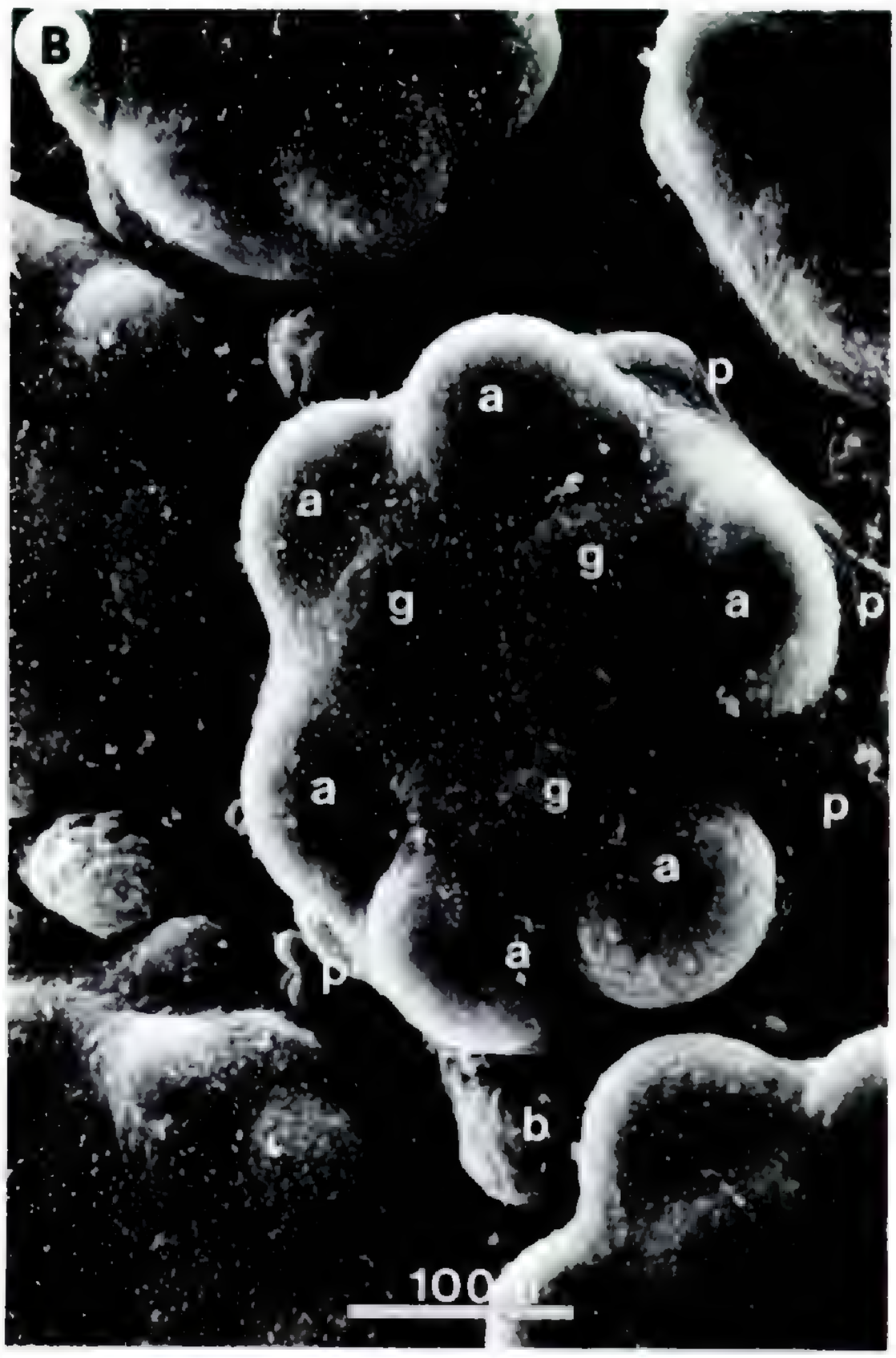
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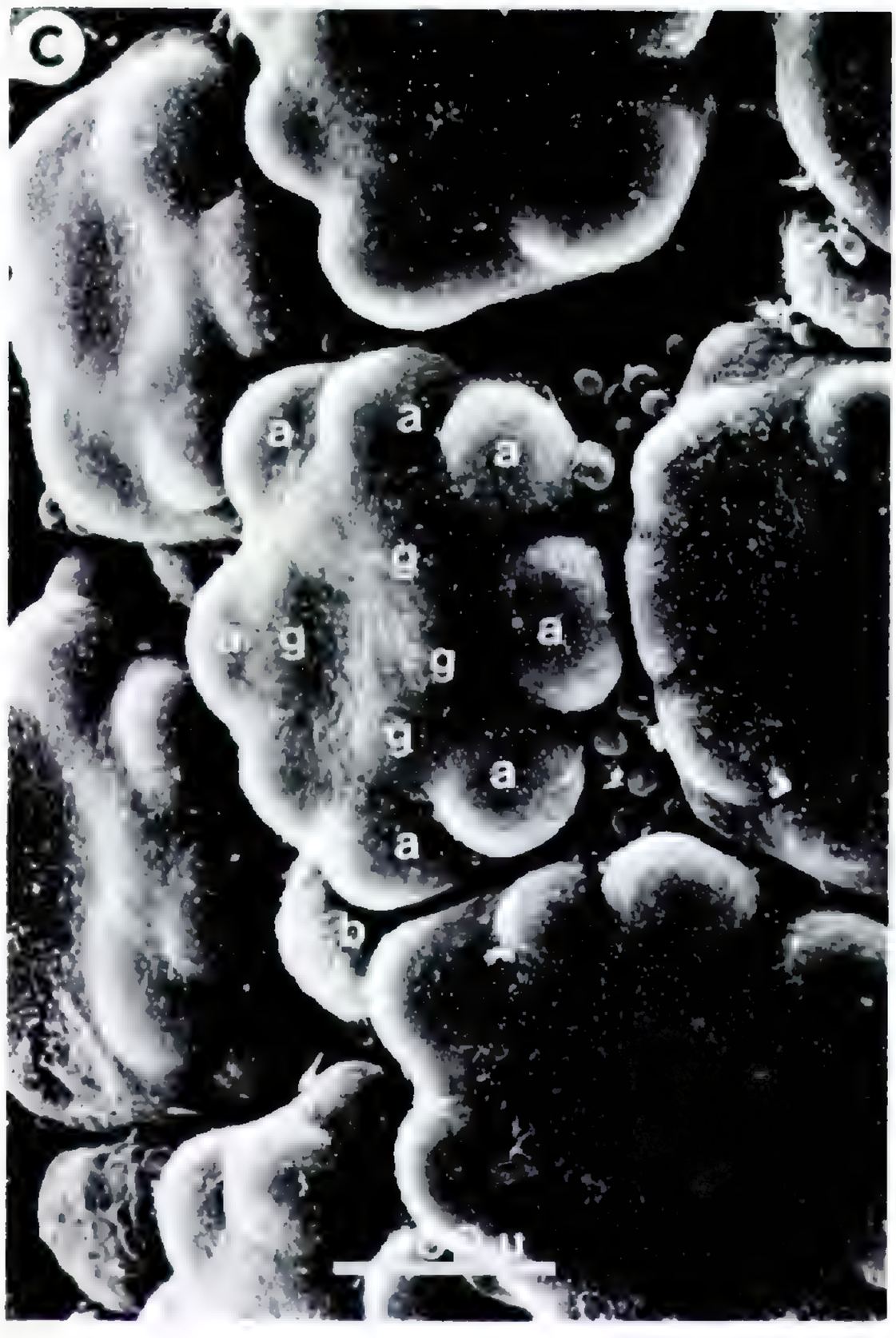
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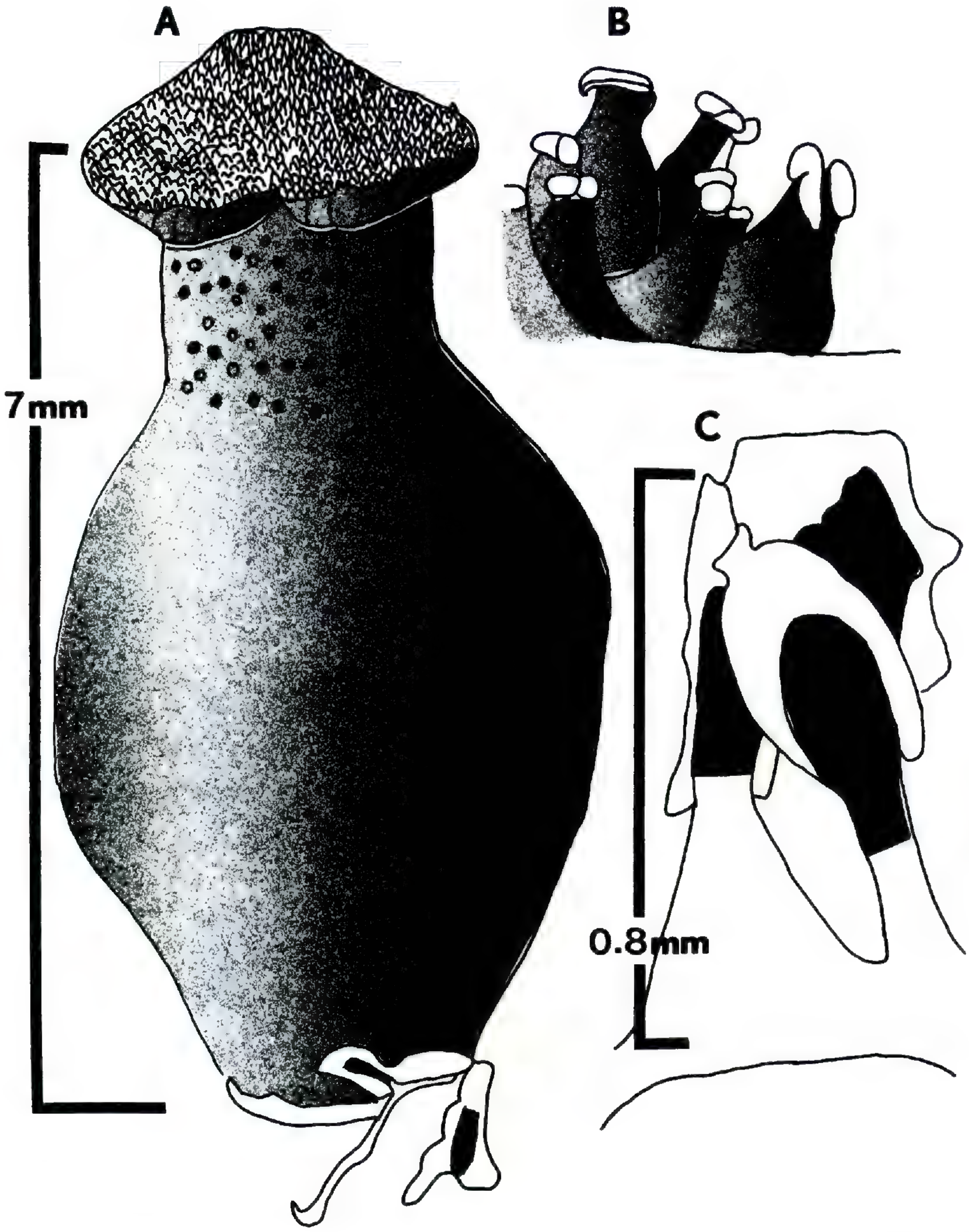

FIGURE 14. Gynoecial structures of *Freycinetia reineckei*.—A. Mature gynoecium with bilobed stigma, gland dots on ovary neck, and staminodia at ovary base.—B. Aspect of gynoecia on surface of spike.—C. Detail of staminodia.

(level 3), which may be either monomorphic or dimorphic, is the spike together with its subtending bract (Fig. 15c). Within each spike is found the fourth modular level (level 4), the floral unit subtended by a tiny bract (Fig. 15d), which could be sexually monomorphic or dimorphic.

For a *Freycinetia* species to be dioecious, i.e., sexually dimorphic at modular level 1, all lower modular levels also must be dimorphic. However, recent field research has revealed some individuals of *F. reineckei* in Samoa to be hermaphroditic at level 3 by producing hermaphroditic spikes (Cox, 1983), as are some individuals of *F. strobilacea* in Indonesia (Cammerloher, 1923; Stone, 1971).

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FIGURE 13. Floral organogenesis in *Freycinetia arborea*.—A. Early developmental stage of flower with subtending bract (b), perianth primordia (p), and androecial primordia (a).—B. Later stage of development showing gynoecial primodia (g).—C. Subsequent developmental stage showing cessation of perianth development, and coalescence of gynoecial primordia into staminode.—D. Later stage showing several flowers along spike. Gynoecia, bracts, and perianth members have all ceased development with only androecial members continuing growth.

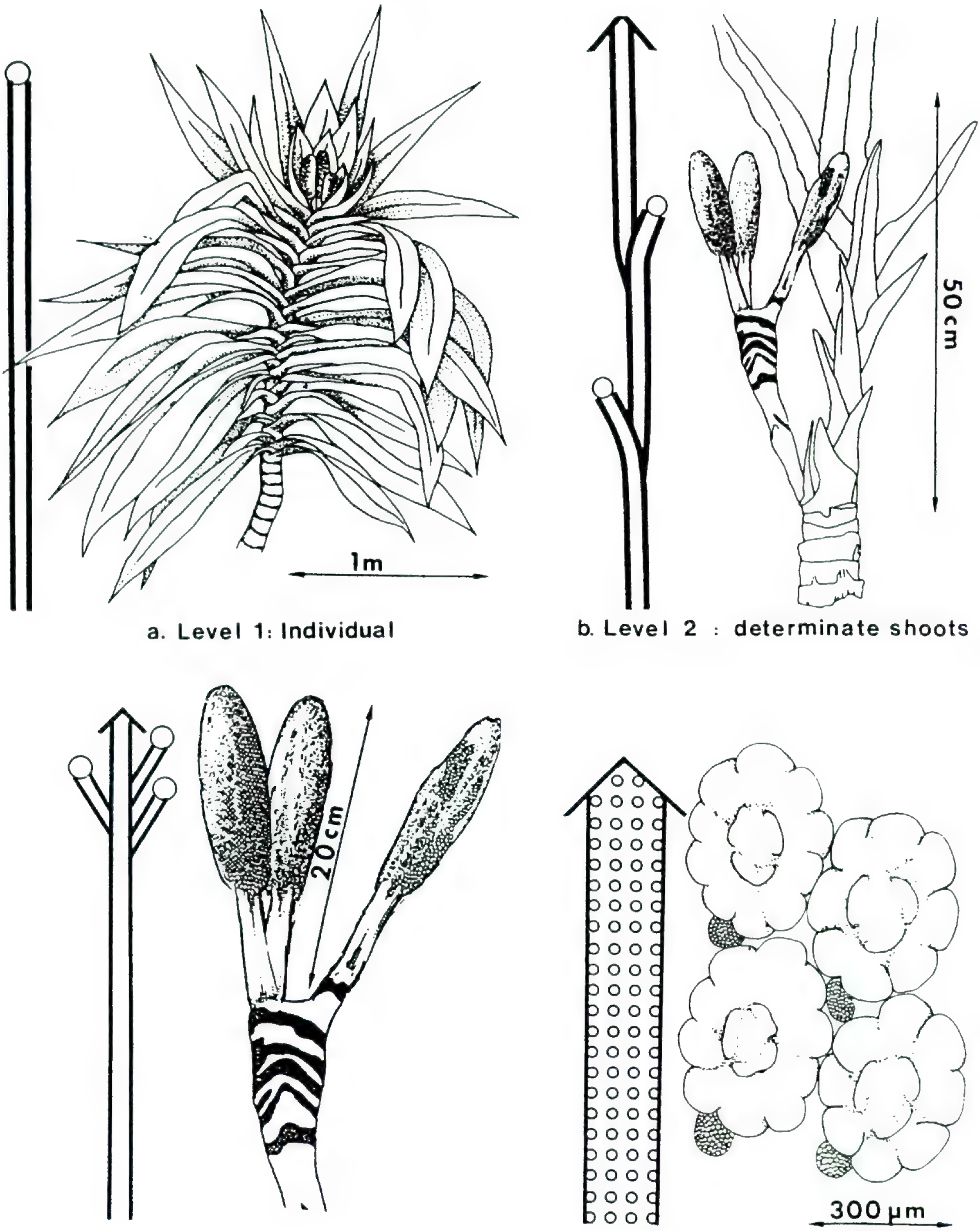

FIGURE 15. The different modular levels in *Freycinetia reineckei* at which various dimorphic or monomorphic reproductive strategies could be expressed. The floral primordia in (d) occur early during organogenesis; crowding on the mature axis obscures individual floral units, particularly on staminate spikes.

Some individuals of *F. scandens* in Australia are hermaphroditic or monomorphic at level 1 by producing male and female shoots on the same plant (Cox et al., 1984); sexual monomorphism at this level is usually termed "monoecism." Similar cases of monoecism were described by Stone (Stone, 1972c; Cox, 1981) in individuals of *Freycinetia imbricata* in Sumatra and *Freycinetia negrosensis* in the Philippines, which also produce staminate and pistillate shoots on the same plant. Such divergences from a dioecious breeding system may be important in island colonization (Baker & Cox, 1984), particularly since monoecious individuals of *Freycinetia scandens* have been found to be self-compatible (Cox et al., 1984). Bagging and exclusion experiments for several species of *Freycinetia* indicate that apomixis is absent (Cox, 1983, 1984).

Pollination biology. *Freycinetia* inflorescences are adapted to pollination by several kinds of vertebrates such as flying foxes (Burck, 1892; van der Pijl, 1956; Cox, 1982, 1984); smaller bats (Knuth & Loew, 1904; Daniel, 1976); squirrels (Heidi, 1927); crows (Cox, 1983); pigeons (Cox, 1984); honeycreepers (Cox, 1983); and white eyes (Cox, 1983); but not rats (Cox, 1983). The openness and availability of the inflorescence to a wide taxonomic variety and size range of pollinators suggest a lack of tightly coupled plant-pollinator coevolution. Indeed, *Freycinetia* pollinators tend to be frugivores. Biochemical assays of *Freycinetia reineckei* inflorescences and a variety of indigenous Samoan fruits eaten by its major pollinator, *Pteropus samoensis*, revealed striking similarities between hexose/disaccharide ratios and amino acid compositions (Cox, 1984). In contrast to pollination systems that are believed to have coevolved in other plants, no apparent evolutionary response of pollinators to *Freycinetia* has been found. There is, however, strong evidence that pollinator behavior has affected the evolution of breeding systems in *Freycinetia*.

The vertebrate pollinators of *Freycinetia* tend to be destructive. For example, the flying foxes that pollinate *Freycinetia reineckei* in Samoa and Guam, *Pteropus samoensis* and *P. mariannensis*, respectively, eat the inner and outer staminate and pistillate bracts as well as the lipid-rich staminate spikes (Fig. 6c, d). Pistillate spikes, which are green and mucilaginous, are rarely disturbed and set abundant seed when pollinated. Although staminate spikes transmit their genes via pollen on the pollinators' faces, and pistillate spikes transmit their genes via ovules, hermaphroditic individuals lose a large proportion of their investment in gynoecial structures due to pollinator damage, and they have a low fitness, represented by a concave fitness set (Cox, 1982). Quantitative comparison of the fitnesses of staminate, pistillate, and hermaphroditic individuals shows vertebrate pollination maintains the dioecious breeding system in *Freycinetia reineckei* (Cox, 1982).

Dispersal. The infructescences of *Freycinetia* are usually brightly colored, frequently red, and are rich in sugars. These attributes make them attractive to various birds and perhaps some flying foxes. *Freycinetia reineckei* in Samoa is dispersed by *Aplonis artifuscus* (Sturnidae). *Fauna Hawaiiensis* (Perkins, 1902) is filled with references to birds of various genera eating *F. arborea* fruits. Guppy (1906) believed birds to be the primary dispersers of *Freycinetia* species and reported finding bird pellets below the inflorescences filled with *Freycinetia* seeds. Experiments on seed germination (Cox, unpublished) suggest adaptation to endozoochoric dispersal, since *F. reineckei* seeds require a mild acid treatment for successful germination. Dispersal by flying foxes is undoubtedly important as well. The type specimen (at BISH) of *Freycinetia degeneri* (*Degener 15128*) has written on the label, "fresh roots pounded as roofs to build their grass houses. They do not eat fruit. Flying foxes eat it." Smith (1979) also believed flying foxes to be important dispersal agents in Fiji. Terrestrial mammals also probably aid dispersal; Perkins (1902) reported that rats eat *F. arborea* in Hawaii, and they are implicated as seed dispersers in New Zealand. A specimen of *F. banksii* (*Meebold 18245*) has written on the label, "eaten by rats," which Daniel (1973) confirmed. The attractiveness and availability of *Freycinetia* infructescences to a wide variety of vertebrates has perhaps been best stated by Stone (1970, pp. 85–86): "Probably the fruits—technically berries—are dispersed by birds, bats, and possibly other mammals. Being juicy, they are edible."

PANDANUS

Floral biology. Stone (1968b) grouped pistillate inflorescences of *Pandanus* according to whether the cephalia are solitary or multiple, and whether the fruits are free or connate into syncarps. In species with single cephalia (e.g., *P. tectorius* sensu latissimo, *P. leram*, Stone, 1983), numerous chartaceous bracts, usually pale yellow or white, are produced beneath the inflorescence and are inserted tristichously. In species with multiple cephalia (e.g., *P. nepalensis*, *P. spinistigmaticus*),

FIGURE 16. *Pandanus tectorius*.—a. Habit in Maui.—b. Staminate inflorescence in Moorea.

the cephalia are borne on racemes, and beneath each cephalium is a single bract. *Pandanus* species in general do not show the extreme telescoping of the main inflorescence internode that occurs in *Freycinetia*, although the cephalia themselves reveal much telescoping of secondary and tertiary axes. Staminate inflorescences of *Pandanus* usually consist of panicles of staminate spikes, each spike subtended by a large, often pale-colored bract. Floral units homologous to those found in *Freycinetia arborea* have yet to be discovered in *Pandanus*, but those of *P. androcephalanthos* and other species of subg. *Martelidendron* in Madagascar perhaps have a similar construction. Stamens are usually fasciate in phalanges, pistillodia infrequently occur (e.g., *P. douglasii*, Stone, 1968b), but tepals have yet to be identified. Similarly, staminodia infrequently occur in pistillate *Pandanus* individuals (e.g., *P. cominsii*, Stone, 1968b), but again tepals have yet to be identified. Detailed studies of floral organogenesis in *Pandanus* are needed.

Pandanus inflorescences, particularly staminate inflorescences (Fig. 16), sometimes have a subtle, pleasant fragrance. Indeed, staminate inflorescences of cultivated *P. odoratissimus* are used in India as a base for perfumes, the "oil of Keura" (Purseglove, 1972). Neither sex, however, produces nectar, and fleshy bracts similar to those found in *Freycinetia* are unknown.

Breeding systems. A true departure from strict dioecism in *Pandanus* has yet to be found. Given the widespread occurrence of staminodia and pistillodia (Stone, 1968b) in the genus, however, it seems likely that further field studies will reveal aberrations. For example, Stone (1972b) found two pistillate individuals of *Pandanus cominsii* var. *Augustus* on Buka Island that had drupes surrounded by staminodia, some of which had anthers; *P. microcarpus* produces staminodia with anthers adnate to the exocarp (Vaughn & Wiehe, 1953). Departures from strict dioecism, if they occur, either are extremely rare or are limited to certain species; I have yet to find, despite extensive searches throughout Polynesia, a single individual of *Pandanus tectorius* that produces both staminate and pistillate inflorescences.

Bagging experiments in Kauai and Maui, Hawaii, and Moorea (French Polynesia) indicate that

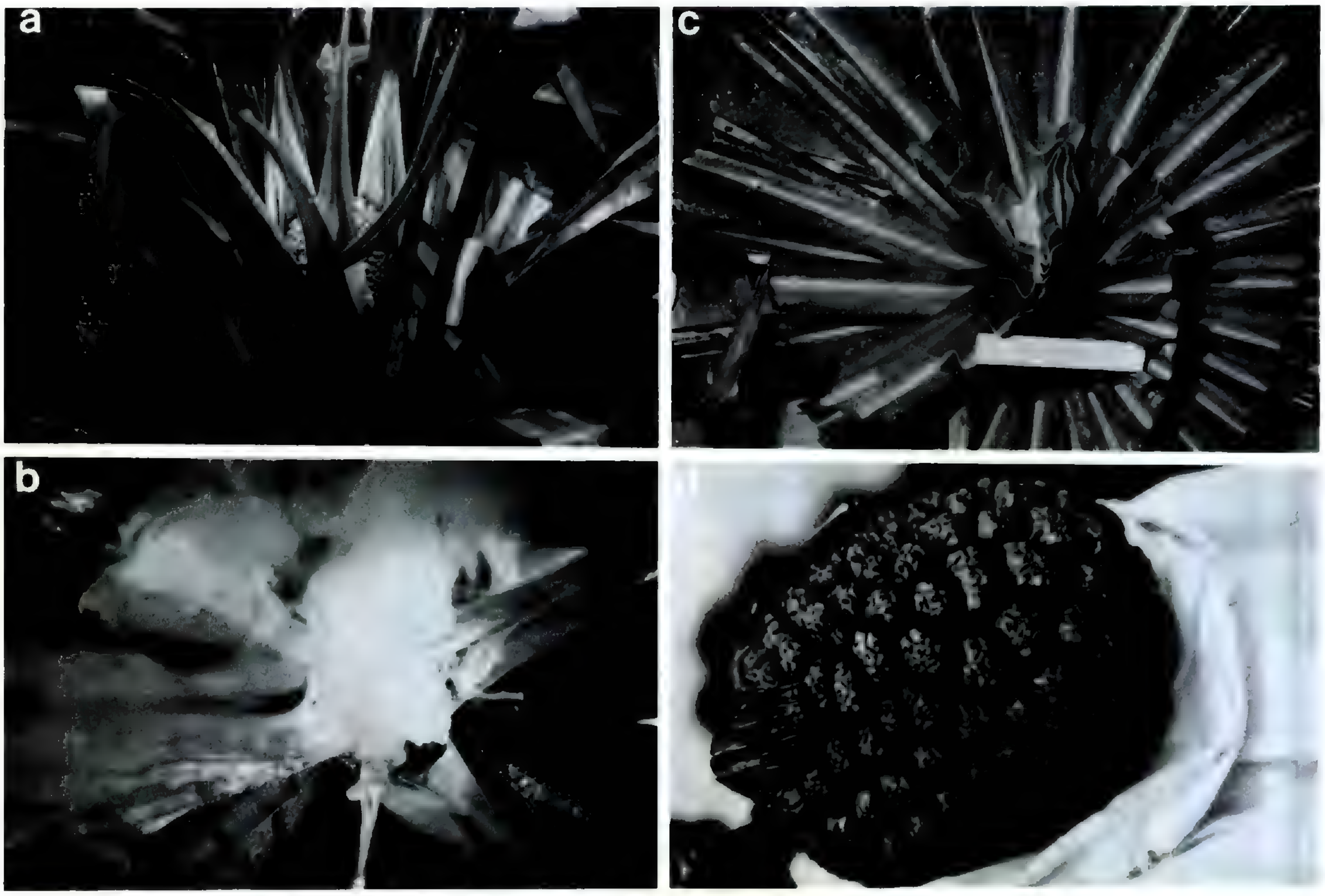

FIGURE 17. *Pandanus tectorius*. —a. Pistillate inflorescence. —b. Flow visualization in field showing deceleration near cephalium. —c. Tristichous phyllotaxis with secondary spiral. —d. Bagged cephalium indicating apomictic nature of breeding system.

Pandanus tectorius is facultatively apomictic (Cox, 1985). All bagged inflorescences produced fruit (Fig. 17). Possibility of contamination of the bags was checked with scanning electron microscopy of stigmatic surfaces; no pollen grains were found. Parthenocarpic fruit development was rejected since bagged cephalia produced viable embryos and endosperm. To determine whether apomixis was obligate or facultative, the genetic diversity of samples of endosperm from bagged and unbagged cephalia was studied with starch gel electrophoresis (Cox, 1985). Five different loci were examined. Endosperm samples from different syncarps from the same unbagged cephalium had significant isozyme diversity, while endosperm samples from syncarps from the same bagged cephalium were monomorphic at all loci. Thus the system is facultatively apomictic, with asexual reproduction occurring in the absence of pollination. Campbell (1911) noted migration of somatic nuclei into the embryo sac, which was confirmed by Cheah & Stone (1975), who found supernumerary nucellar nuclei in the embryo sac of *Pandanus parvus*. Facultative apomixis may occur throughout the genus; as early as 1867 Kurz found isolated *Pandanus dubius* females to produce fruit, while Fagerlind (1940) reported apparent parthenocarpy in *Pandanus columniformis*. I have found in the Royal Botanic Gardens, Sydney, a sole pistillate individual of *Pandanus forceps* that sets abundant fruit, and in the Royal Botanical Garden, Melbourne, a single pistillate individual of *Pandanus forsteri* that also produces copious fruit; whether this indicates apomixis or parthenocarpy remains to be determined.

Pollination biology. The pollination biology of nearly all species of *Pandanus* remains unstudied. I have made an extensive study, however, of the pollination ecology of *Pandanus tectorius* sensu latissimo in Hawaii and French Polynesia (Cox, 1985). Although insects (e.g., bees) are frequent visitors to staminate inflorescences where they gather pollen, they seldom visit pistillate inflorescences. Neither type of inflorescence produces nectar or any pollinator reward other than pollen. Peroxidase assays indicate an early onset of stigmatic receptivity that extends until well after fruit formation. The copious pollen produced by the pendulous, paniculate staminate inflorescences (Fig. 16b) is devoid of a *pollenkitt* and blows easily in the wind. However, a *pollenkitt* occurs in other species; according to Stone it is formed in *Pandanus beccarii* and similar species of sect. *Maysops*. To test for wind pollination, flow patterns

around pistillate inflorescences were examined with a laboratory wind tunnel using the techniques of Niklas (1982), and in the field using a portable smoke-injection apparatus (Cox, 1985). Regardless of inflorescence orientation, flows in the range of 1 m/sec. resulted in back eddies that caused significant deceleration in the region of the stigmatic surfaces (Fig. 17b). Spiral patterns in the xy and xz planes indicated that pistillate *Pandanus tectorius* inflorescences function as highly efficient pollen receivers, being hydrodynamically analogous to some filter-feeding marine invertebrates. This anemophilous nature of *P. tectorius*, together with its system of facultative apomixis, was confirmed through bagging studies.

Dispersal. The primary unit of dispersal on most *Pandanus* species is the syncarp, frequently termed a phalange.[3] The phalanges are brightly colored, and the basal part is sweet. In coastal species, such as *P. tectorius*, the phalanges are buoyant and can frequently be found in beach-drift throughout the Pacific (Gunn & Dennis, 1976). Guppy (1906) and Ridley (1930) considered *P. tectorius* to be dispersed primarily by ocean currents, although Lee (1985) reported localized dispersal by crabs. Bird dispersal of *P. tectorius* also occurs in Samoa, and flying fox dispersal has been observed in Micronesia (Stone, pers. comm.).

Stone (1982a, pers. comm.) reported turtle dispersal of *P. helicopus*, a freshwater species, in the Malay Peninsula, and endozoochoric dispersal of inland species is highly likely (Stone, 1982a). Dispersal by humans of economically useful species has occurred as well.

In Hawaii a census of four 0.25-m^2 plots of *P. tectorius* phalanges lying on the ground revealed that of those phalanges that produce seedlings, 69% produce two–six seedlings (Cox, 1985). Using data from this survey, a probability analysis revealed that the likelihood of any established phalange producing at least one male and one female seedling exceeds 55% (Cox, 1985). Further work by Lee (1989) in Moorea has confirmed that the dispersal of a single phalange may establish a sexually reproductive population.

[3] Terminology follows Stone. The levels employed are (1) carpel, (2) phalange, and (3) cephalium. Older works use syncarp, but this can refer to either level 2 or 3. Each carpel ripens to form a drupe; in species with free or solitary drupes, the cephalium consists of drupes. However, in species such as *P. tectorius*, each phalange is formed of several connate drupes; hence the term "polydrupe" is sometimes used.

SARARANGA

Floral biology. The massive (up to 1.7 m long) pendulous inflorescences of *Sararanga* are always terminal (Figs. 14c, 15a), with renewal growth occurring through the development of axillary buds beneath the inflorescence. In contrast to *Freycinetia* and *Pandanus*, the pistillate inflorescence is strongly paniculate while the staminate inflorescence consists of panicles of staminate heads, similar to that found in *Pandanus* species. Both types of inflorescences are subtended by small, hard bracts. The nature of the terminal floral unit in *Sararanga* remains unclear. The green, terminal floral units (Fig. 7d) are composed of numerous fused carpels, each producing a single anatropous ovule beneath a single pointlike stigma. The sinuous arrangements of the fused carpels and their stigmas "strongly resemble the [pattern of] stitching on an American baseball" (Stone, 1961). A small, whitish cuplike structure is produced at the base of the fused carpels. This structure, when analyzed by paper chromatography, proves to be rich in hexose sugars. Although the terminal floral units were termed "receptacula florifera" by Hemsley (1893), Stapf (1896) called them flowers, a practice followed by Stone (1961), who considered the terminal floral units "pedicellate flowers" with the white cupule termed a "perianth." North & Willis (1971) described the fertilized terminal floral units as "fleshy fruits, consisting of numerous carpels."

However, precise homology between the terminal floral units of *Sararanga* and floral structures of other Pandanaceae, as well as other monocotyledons, remains obscure. Studies of floral organogenesis previously described revealed little similarity between the terminal floral units of *Sararanga* and the flowers of *Freycinetia*. Particularly unclear is the nature of the white cupule that subtends the terminal floral unit. This cupule scarcely resembles the perianth of any other monocotyledonous flower; it is much more bractlike in appearance. Ultimate resolution of these difficulties requires, in my opinion, study of the ontogenetic development of these structures; as yet, however, I have been unable to obtain the appropriate developmental stages (Fig. 18). Based on current information, the possibility that the terminal floral unit of *Sararanga* may be homologous to a *Pandanus* phalange, or even homologous to an entire *Pandanus* cephalium or *Freycinetia* spike, with the cupule representing the subtending bract, cannot be excluded. The fleshy cupule appears to serve the same function, as pollinator rewards, as the fleshy bracts of *Freycinetia*. Analysis of the cupule

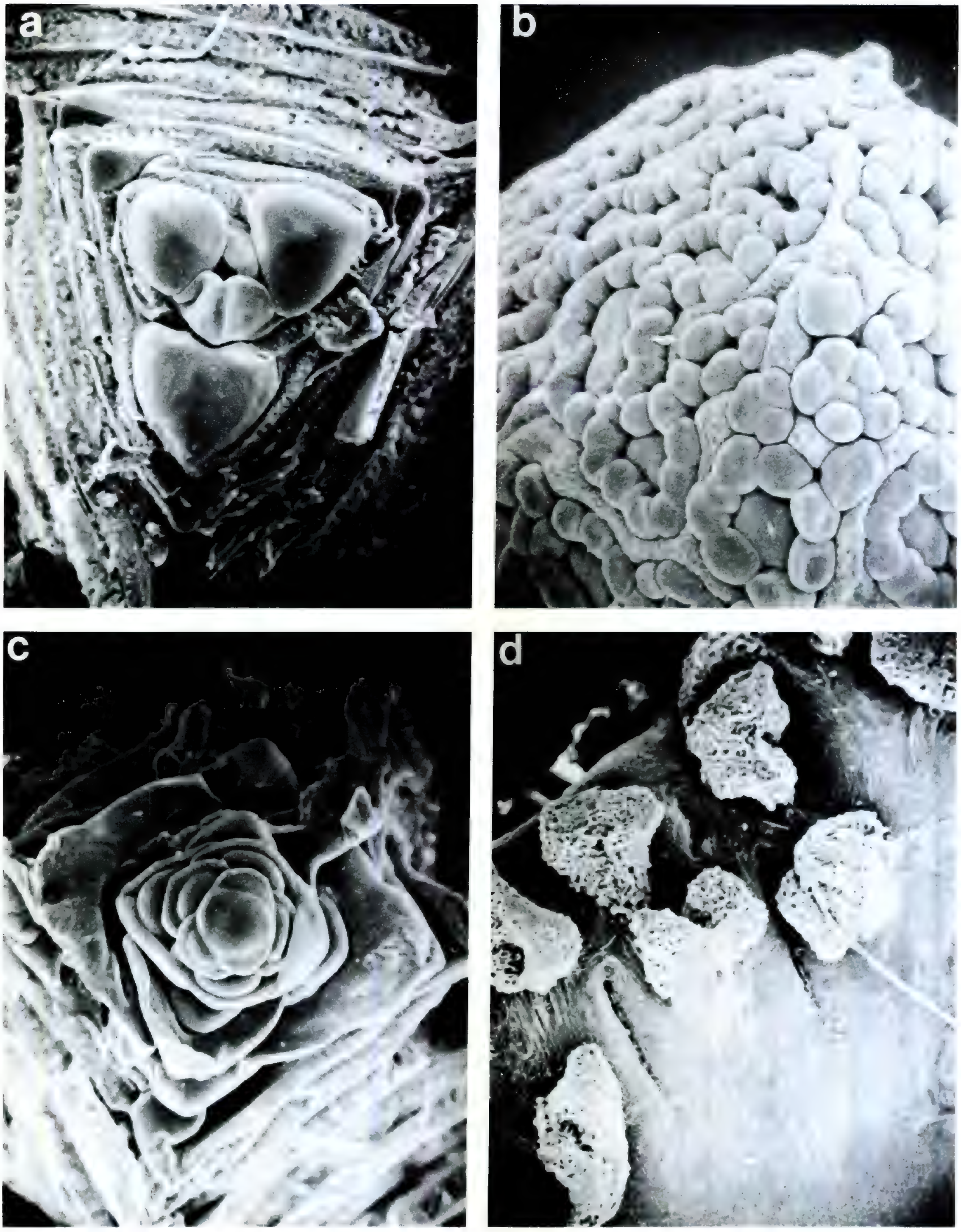

FIGURE 18. Floral organogenesis in *Freycinetia* and *Sararanga*.—a. Dissection of reproductive apex of *F. reineckei* showing young spikes and subtending bracts.—b. Early developmental stage of a staminate *F. reineckei* spike.—c. Dissection of *Sararanga sinuosa* reproductive staminate apex from a secondary axis showing early stages of inflorescence development; note decussate nature of phyllotaxis.—d. Stigmatic surfaces of *Sararanga sinuosa* cephalium.

reveals it to be similar to *Freycinetia* bracts by being very rich in hexose sugars. Since *Sararanga* produces no nectar or other pollinator reward, these white, fleshy cupules serve as the sole pollinator reward. They are, however, extremely small in comparison with the hexose-rich bracts of *Freycinetia* or the bracts of *Pandanus* inflorescences.

Breeding systems. I have surveyed populations of *Sararanga sinuosa* in the Konnga Region of Guadalcanal Island, Tulagi Island, and along the Siota Passage on Big and Little Ngela islands and have yet to discover any departures from strict dioecism. Staminodia and pistillodia are unknown in the genus.

Sararanga sinuosa does not appear to be apomictic, as some isolated trees have very poor or no fruit set, and within any particular inflorescence, numerous terminal floral units fail to develop. An isolated pistillate tree in the Honiara Botanical Gardens, Guadalcanal, sets some fruit, although the set is poor compared with wild trees. Because of deforestation, this individual is at least 6 km from any other possible conspecific and 15 km from any other known conspecific. Even this does not, however, provide evidence for apomixis or parthenocarpy, since, as will be discussed below, *Sararanga sinuosa* appears to be entomophilous. As Kerner von Marilaun (1895, p. 208) reported, a *Dracunculus creticus* (Araceae) planted in the Vienna Botanic Gardens attracted at anthesis a swarm of dung beetles when previous to its opening none could be found anywhere in the Gardens or immediate vicinity. The possibility that the massive inflorescences of *Sararanga*, which rival those of the monocarpic palms in size and productivity, could attract pollinators from several kilometers away cannot be discounted.

Pollination biology. The pollen grains of *Sararanga sinuosa* average 13 μm in diameter, have reticulate exines (Figs. 15b, 18d), and lack a *pollenkitt*. The anthers are borne in groups, each of which is subtended by a small fleshy bractlike cupule nearly identical to that produced beneath the pistillate terminal floral units. As mentioned above, this cupule or bract is rich in hexose sugars. The entire staminate inflorescence has a slightly peppery smell; no similar odor can be detected from the pistillate inflorescences. The sessile stigmas of the pistillate floral units, borne in sinuous rows (Fig. 7d, 18d), show peroxidase activity while the unit is small and green. In staminate and pistillate inflorescences no nectar is produced; the sole pollinator rewards are pollen and the whitish, hexose-rich cupules or bracts that subtend the floral units.

Since the inflorescences are pendulous from the tops of these tall (20 m) trees, determination of floral visitors is difficult. I have witnesed small beetlelike flying insects visiting the pistillate inflorescences but have not captured any for identification and analysis. A night I spent in the crown of an *S. sinuosa* tree in Tulagi Island similarly failed to yield any evidence of nocturnal visitors. Wind tunnel analysis of flow patterns around pistillate inflorescences indicated no significant eddies or flow patterns produced by the inflorescence or by the terminal floral units that cause flow deceleration near the stigmatic surfaces. I therefore believe *Sararanga sinuosa* to be pollinated solely by flying insects, although further fieldwork in the Solomons is needed to gain more details of the pollination ecology of *Sararanga*.

Dispersal. Guppy (1906, p. 156) believed *Sararanga sinuosa* to be bird-dispersed. Although I have yet to witness dispersal, the bright red (A. D. E. Elmer called them "candy red") terminal floral units, which are rich in disaccharides, have a delicious taste reminiscent of cherries or strawberries. Given the position high in the trees, they are almost certainly dispersed by birds and bats, although confirmation of this awaits further fieldwork.

Breeding Systems, Evolution, and Systematics

In principle, the phylogenetic tree derived from systematic information can be used to interpret evolutionary trends in breeding system and pollination syndromes in the three genera of Pandanaceae. For example, because pollination syndromes appear to be relatively constant within each genus (with the exception of possible chiropterophily in some species of *Pandanus* sect. *Maysops*), and since each pollination syndrome obviously has an evolutionary history, the genera can be replaced with their respective pollination syndromes as shown in Figure 19. This modified cladogram indicates that within Pandanaceae, wind and insect pollination have evolutionary histories more closely related to each other than either does to vertebrate pollination. Only a few details concerning possible trends in pollination biology can be derived from the consensus tree, however, since information from pollination biology was not used to derive the tree. Unfortunately, the pollination biologies of three genera I have used as outgroups, *Balaka*, *Rhaphidophora*, and *Asplundia*, remain unknown. However, to illustrate the possibility for interpreting the evolution of breeding systems and pollination syndromes, should the sister group of the

Pandanaceae be convincingly demonstrated, I substitute for *Asplundia* in Figure 20 the genus *Cyclanthus* (Cyclanthaceae) whose pollination biology has been well studied (Beach, 1982).

In Costa Rica, *Cyclanthus bipartitus* is pollinated primarily by beetles (Beach, 1982). The first night after pistillate anthesis, scarab beetles of the genus *Cyclocephala* forage on the lipid-rich fleshy adaxial surfaces of the inner bracts. Later, after staminate anthesis, the beetles feed on the pollen.

If we put these details on the cladogram (Fig. 19), we find *Cyclanthus* and Pandanaceae sharing two features of pollination biology as a symplesiomorphy: fleshy bracts and pollen used as pollinator rewards. A synapomorphy distinguishing Pandanaceae, is tristichous phyllotaxis, which imparts a radial symmetry. Of importance to the pollination biology of *Pandanus*, this phyllotactic pattern positions the bracts in three ranks beneath the inflorescence. Wind tunnel experiments on *Pandanus* showed such tristichy of the bracts to impart aerodynamic characteristics necessary for pollen capture by the pistillate inflorescence (Cox, 1985). Although highly functional, this feature cannot be considered adaptive in the strict sense since pistillate inflorescences of vertebrate-pollinated *Freycinetia reineckei* also produce similar flow patterns when placed in a wind tunnel. Given the cladogram here derived, tristichous phyllotaxis appears as a preadaptation to anemophily that was possessed by some of the ancestral pandans, and proved functional only after changes in the staminate inflorescence, such as lengthening of the internode, allowed pollen to be wind-dispersed.

It is of interest that a synapomorphy characterizing *Sararanga* and *Pandanus* is relatively elongated internode length in the staminate inflorescence. This results in a pendulous inflorescence that facilitates dispersion of pollen on the wind. As shown by the wind tunnel experiments with *Freycinetia*, the ancestral tristichy of the family made the involucrate pandanaceous inflorescence ready to function as an aerodynamically efficient pollen receiver. Thus, merely lengthening the staminate inflorescence internode made a jump from vertebrate pollination to wind pollination suddenly possible. With the advent of wind pollination, production of pollinator rewards became unnecessary. Here the change of fleshy bracts to chartaceous bracts appears as an autapomorphy characterizing *Pandanus*.

A possible autapomorphy characterizing *Freycinetia* is a lipid-rich *pollenkitt* that holds pollen to the feathers of birds and to the facial hairs of flying foxes as well as providing a pollinator reward

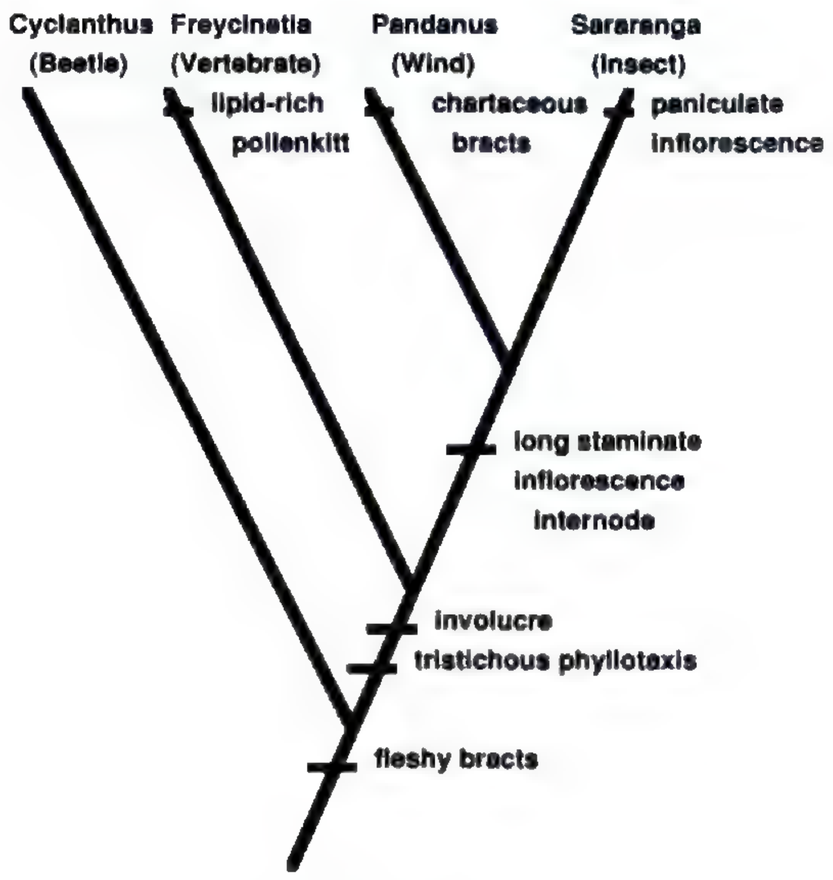

FIGURE 19. Consensus tree of pollination syndromes in Pandanaceae with *Cyclanthus* (Cyclanthaceae) used to determine polarities.

(Cox, 1984). A *pollenkitt*, however, also occurs in *Pandanus* (in *P. beccarii* and perhaps other species of sect. *Maysops*).

The characteristics of vertebrate-pollinated pandanaceous inflorescences, as revealed by extant *Freycinetia* species, make them unlikely to be pollinated by insects. For example, the open involucres cause the head of a large vertebrate pollinator, such as a bird or flying fox, to come into direct contact with the spikes as they feed on the bracts. Contact with the spikes would not be made, however, by small insects feeding on the bracts, given the distance between the attractive bracts and the spikes. Thus, even though pollen could be deposited on insects that fed on the staminate spikes, this pollen would not be transferred effectively to pistillate spikes, given the lack of nectar or other pollinator rewards offered by the pistillate spikes themselves. A reduction in size of the inflorescence resulting in closer spatial proximity of the pollinator reward to the stigmatic surfaces would be necessary for insect pollination to occur.

Something similar appears to have occurred in *Sararanga*, pending, of course, accurate determination of the morphological identity of the terminal floral units. The inflorescence is paniculate and massive, creating a large display for potential insect pollinators. The basal hexose-rich cupule or bract is positioned on the pedunculate terminal floral unit so that the body of any insect feeding on it would come in contact with the sessile stigmas. The cupule or bract of the staminate terminal floral units is in a similar position, and would thus deposit pollen in a similar manner on the body of any insect feeding on the bract.

Thus, if the Cyclanthaceae indeed proved to be the sister group to the Pandanaceae, an evolution-

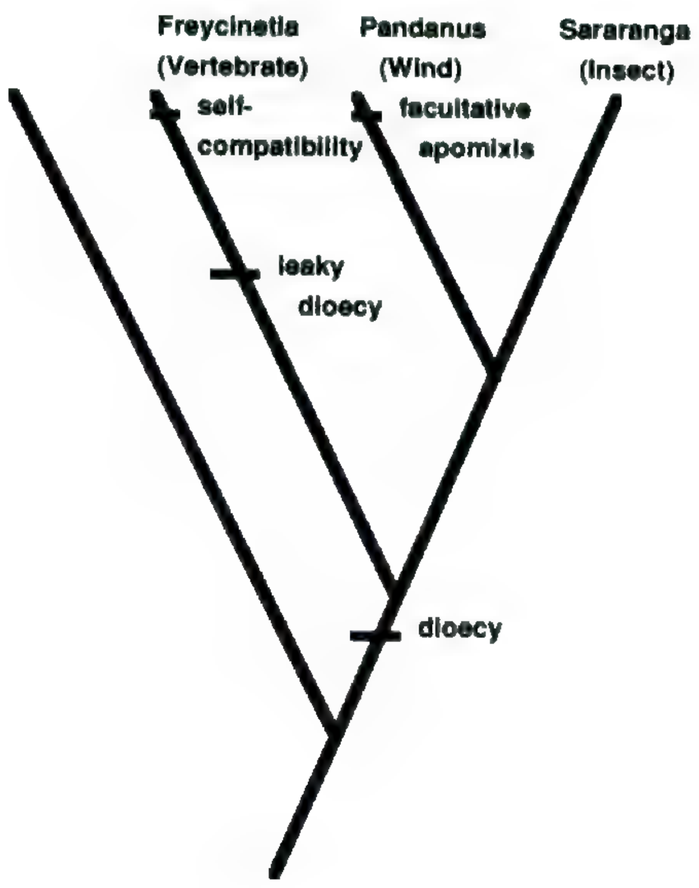

FIGURE 20. Consensus tree of Pandanaceae with primary breeding systems superimposed; polarities determined as in Figure 5.

ary sequence from vertebrate pollination to a branching point between wind pollination and insect pollination could be envisioned.

In terms of breeding system evolution, *Cyclanthus bipartitus* is monoecious, with unisexual flowers produced in alternating cycles on the congested spadix. Because, as shown in extant hermaphroditic *Freycinetia* inflorescences (Cox, 1982), vertebrate pollinators feeding on pollen cause significant damage to gynoecial structures, the advent of vertebrate pollination would cause a monomorphic (hermaphroditic) population to become vulnerable to invasion by dimorphic (dioecious) mutants (Cox, 1982, 1986). Thus dioecism, which is a synapomorphy uniting Pandanaceae (Fig. 20), may have evolved in the family in response to ancestral vertebrate pollination. Similarly, vertebrate pollination maintains dioecism in *Freycinetia* populations today (Cox, 1982). Dioecism, however, greatly reduces colonization ability (Baker & Cox, 1984). Thus, the evolution of facultative apomixis in *Pandanus* increased its ability to colonize new habitats and islands, resulting in a dramatic range extension. Dioecism may be maladaptive in relation to colonization potential in *Sararanga* because it reduces likelihood of successful pollination, and thus may partially account for its inability to colonize oceanic islands successively.

The relationships between breeding systems, pollination syndromes, ranges, and numbers of species may be highly significant in the Pandanaceae. For example, the genus *Pandanus*, with wind pollination, facultative apomixis, and water- or animal-dispersed syncarps, has the broadest range and greatest number of species. *Pandanus*, with its anemophilous pollination system, can colonize any appropriate island regardless of the island's faunal composition. Since *Pandanus* is facultatively apomictic, successful colonization does not require the establishment of both sexes. Thus a single female propagule may eventually fill an entire island with its apomictic progeny. Through founder effect and genetic drift alone, such facultative apomixis in a plant colonizing disparate islands would be expected to result in a huge range and a massive number of species. Indeed this breeding system may partially explain some of the controversies in *Pandanus* taxonomy. For example, Stone (1976a, 1982c) and Fosberg (1977) have frequently disagreed with St. John (1979a, b) on the identity of *Pandanus tectorius*. Fosberg, for example, reduced six binomials erected by St. John from Aldabran specimens to synonymy with *Pandanus tectorius*, and Stone reduced 15 *Pandanus* species erected by St. John from coastal Australian collections to synonymy with *P. tectorius*. As Stone (1982c, p. 135) perceptively suggested, "The obvious taxonomic difficulties in certain species-groups of *Pandanus* such as the '*P. tectorius*' group and also in *Pandanus* section Austrokeura Stone, may be caused by apomixis."

Facultative apomixis and anemophily may also permit *Pandanus* species to colonize new habitats that would otherwise be unavailable to it if it were linked to a specific type or class of animal pollinators. Thus, allopatric speciation processes as well as genetic drift may have contributed to the high speciation rate in *Pandanus*.

Freycinetia species, on the other hand, lack facultative apomixis and water dispersal. However, their attractiveness to a wide variety of vertebrate pollinators and dispersers, as well as infrequent "leaky dioecy" (Baker & Cox, 1984), would assure them a large range and high speciation rate, albeit lower than *Pandanus*, where the apomixis coupled with abiotic dispersal has likely resulted in speciation through genetic drift.

Conversely, *Sararanga* lacks facultative apomixis, "leaky dioecy," and is apparently tied to a single class of pollinators of possibly a limited range, which may explain its small range and low number of species. Its distribution along the edge of the Tethys geosyncline and its absence from oceanic islands suggest that the distribution of *Sararanga* may be entirely due to vicariance processes, i.e., local differentiation resulting in two species.

In conclusion, recognition of the phylogenetic relationships of Pandanaceae can help in the formulation of various hypotheses concerning breeding system evolution, evolution of different pollination syndromes, and their effect on range

extension and speciation rates. In this light, Pandanaceae do not appear to be primarily anemophilous and diclinous, as Meeuse (1972) suggested, but rather they spring from vertebrate-pollinated ancestors that developed dioecism in response to destructive pollinators. Subsequently, there have been interactive effects between pollination, breeding system evolution, speciosity, and range extension, with only a few changes in inflorescence morphology, leading to the evolution of strikingly different pollination syndromes. Obviously this view is limited by the accuracy and resolution of the proposed phylogeny. It is hoped that continued interest in tropical monocotyledons will one day yield persuasive evidence for a sister group to the Pandanaceae. Such a discovery would facilitate rigorous testing of the hypotheses proposed here.

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NOTES

WEBERBAUERA PERFORATA (BRASSICACEAE), A NEW SPECIES FROM PERU

Weberbauera Gilg & Muschler is a South American genus of 16 species distributed along the Andes from northern Peru south into Patagonia. The genus has been recently revised (Al-Shehbaz, 1990), and its boundaries were then expanded only slightly to include three artificially delimited segregates that Schulz (1924) proposed as *Alpaminia* O. E. Schulz, *Pelagatia* O. E. Schulz, and *Stenodraba* O. E. Schulz. As I delimited the genus in 1990, *Weberbauera* is a well-defined, monophyletic genus somewhat related to the South American *Englerocharis* Muschler (2 species), *Onuris* Philippi (5 species), and *Sarcodraba* Gilg & Muschler (3 species). *Weberbauera perforata* Al-Shehbaz was not included in my recent revision of the genus because the collections on which this new species is based were misidentified as *Draba* L.

Weberbauera perforata Al-Shehbaz, sp. nov. TYPE: Peru. Depto. Cuzco: Nevado Auzangate (as Ausangate), [13°48′S–71°14′W], 4,800 m, 17 May 1957, *R. Hirsch P1255* (holotype, GH). Figure 1.

Herba perenna caespitosa pulvinata; folia basalia rosulata spathulata, petiolata, superne et ad marginem sericeis, 1–3 cm longa, 2–6 mm lata; sepala oblonga, lutea, 2–2.5 mm longa; petala late spathulata vel suborbiculata, unguiculata, lutea, 2.5–3 mm longa; siliqua oblonga, 4–7 mm longa, 1.5–2 mm lata; septum incompletum dimidium.

Cespitose, perennial herbs forming dense cushions. Caudex simple or few-branched, densely covered with persistent petioles of previous years. Flowering stems slender, decumbent, falling off at end of growing season. Basal leaves petiolate, rosulate, spatulate, 1–3 cm long, 2–6 mm wide, obtuse to rounded at apex, entire, densely sericeous on the upper surface with trichomes to 2 mm long, ciliate at margin, glabrous beneath; petioles 6–16 mm long, persistent, stramineous, becoming papery. Cauline leaves linear to narrowly oblanceolate, pubescent on the upper surface, 4–12 mm long, 0.5–1 mm wide. Inflorescences few-flowered, corymbose racemes, only slightly elongated in fruit. Sepals oblong, yellow, erect, nonsaccate, glabrous, 2–2.5 mm long, ca. 1.5 mm wide. Petals broadly spatulate to suborbicular, yellow, clawed, 2.5–3 mm long, 1.6–2 mm wide; claws erect, 1.2–1.8 mm long. Stamens tetradynamous; filaments 1.8–2.2 mm long; anthers oblong, 0.6–0.8 mm long. Nectar glands confluent, subtending the bases of all filaments. Fruiting pedicels divaricate-ascending, straight, glabrous or sparsely pubescent, 3–5 mm long. Fruits oblong, glabrous, terete, 4–7 mm long, 1.5–2 mm wide; septum with a central perforation; gynophore 0.3–0.4 mm long; style 0.2–0.3 mm long; stigma entire. Seeds oblong, ca. 1 mm long; cotyledons incumbent.

Additional specimen examined. PERU. DEPTO. CUZCO: Ocangate, [13°38′S–71°24′W], 4,700 m, 11 May 1957, *R. Hirsch P1215* (GH).

Weberbauera perforata is readily distinguished from all other species of *Weberbauera* in having yellow flowers, incomplete septa, and densely sericeous upper surface of basal leaves. The other species of *Weberbauera* have white flowers, complete septa, and differently pubescent basal leaves.

I am most grateful to George K. Rogers for his critical review of the manuscript.

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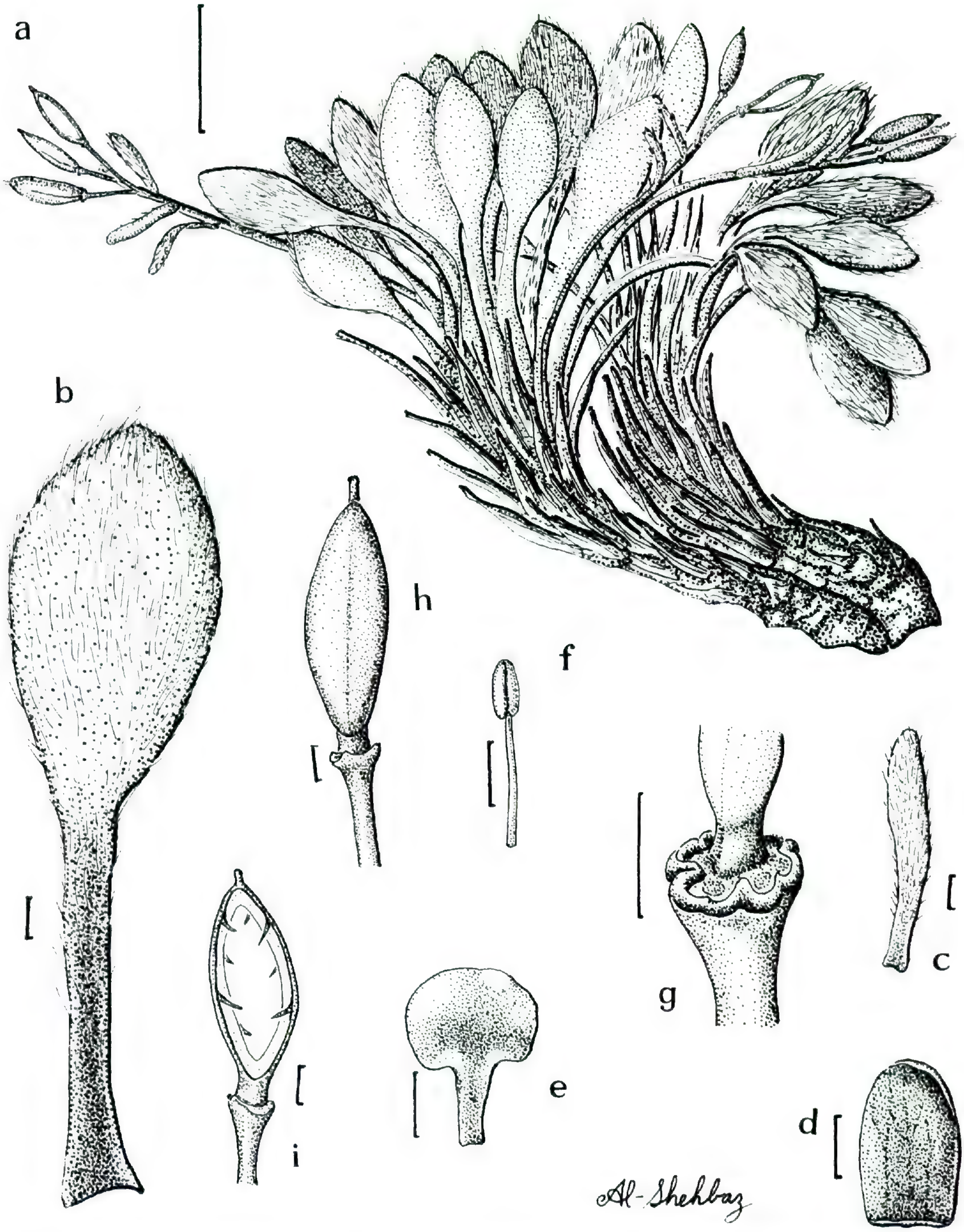

FIGURE 1. *Weberbauera perforata*. —a. Plant.—b. Basal leaf, upper surface.—c. Cauline leaf, upper surface.—d. Sepal.—e. Petal.—f. Stamen.—g. Receptacle with nectar glands.—h. Fruit.—i. Replum and septum. Scales a = 1 cm, b–i = 1 mm. Drawings a–c, h, i, from holotype; d–g from paratype.

BRAYOPSIS GAMOSEPALA (BRASSICACEAE), A REMARKABLE NEW SPECIES WITH GAMOSEPALOUS CALYX

During the preparation of a monograph on the South American species of *Draba* L., a new Bolivian species of *Brayopsis* Gilg & Muschler was discovered. The species, hereafter *B. gamosepala* Al-Shehbaz, is unique among all of the New World members of the mustard family (Brassicaceae) in having typically united instead of distinct sepals.

True and apparent gamosepaly in the Brassicaceae have been previously reported. Hedge (in Hedge & Rechinger, 1968) described *Sisymbrium gamosepalum* Hedge from Afghanistan, but the species has connivent instead of truly connate sepals. Haussknecht (1897) established the genus *Gamosepalum* Hausskn. as distinct from *Alyssum* L. solely on his assumption that *Gamosepalum* has a gamosepalous calyx. Schulz (1936) retained *Gamosepalum* as a distinct genus, but as Dudley (1964) showed, the calyx in this group consists of distinct sepals that falsely appear to be connate because of interlocking idumentum. The only other gamosepalous species of the Brassicaceae was described by Pampanini (1926) as *Desideria mirabilis* Pamp. The species, which Jafri (1973) justifiably transferred to *Christolea* Camb., is endemic to Karakorum, Pakistan. Evidently, gamosepalous calyces evolved independently in *Brayopsis* and *Christolea*.

Brayopsis gamosepala Al-Shehbaz, sp. nov. TYPE: Bolivia: La Paz, Bautista Naavedra, "Kalkrippen etwa 4 km S Kreuzung der Strasse nach Escoma, Felsspalten, Geröll, Feinschutt; Exp.: W; Neigung 15-45 Grad," 4,460 m, 10 Jan. 1980, *J. Krach 7640* (holotype, MO; isotypes, GH, M). Figure 1.

Herba perenna caespitosa scaposa nana; folia basalia rosulata densissime conferta, elliptica vel oblonga, 6–8(–15) mm longa, (1.2–)2–3 mm lata, supra et ad marginem longe villosa; calyx campanulatus, (3–)3.5–4.5(–5) mm longus, sepala connata; petala lineares, 6–7 mm longa, 1.2–1.4(–1.7) mm lata; ovarium pilis appressum dense obtectum; siliquae 7–11 mm longae; styli 1.6–2 mm longi; semina 1 × 0.7 mm.

Cespitose, scapose, small, perennial herbs forming dense cushions. Caudex usually branched, covered with persistent leaf bases of previous years, the branches terminated in rosettes. Basal leaves petiolate, rosulate, 6–8(–15) mm long, (1.2–)2–3 mm wide; blades elliptic or sometimes oblong to ovate, entire, obtuse to subacute, the upper surface and margin sparsely to densely villous with simple trichomes to 2.5 mm long, the lower surface glabrous. Peduncles 1-flowered, sparsely pubescent, 6–10(–15) mm long in fruit. Calyx campanulate, gamosepalous, (3–)3.5–4.5(–5) mm long, sparsely pubescent with short trichomes; teeth broadly triangular, 1–1.8 mm long. Petals linear, 6–7 mm long, 1.2–1.4(–1.7) mm wide, slightly narrowed to base. Stamens tetradynamous, erect, 4–5.5 mm long; anthers narrowly oblong, 1.4–1.8 mm long. Nectar gland ringlike, low, subtending the bases of all filaments. Ovary sessile, densely pubescent with appressed, simple and furcate trichomes. Fruits linear, densely pubescent, 7–11 mm long, ca. 2 mm wide; septum complete; style slender, glabrous, 1.6–2 mm long; stigma capitate, entire. Seeds ovate, subbiseriate, ca. 1 × 0.7 mm.

Brayopsis gamosepala is most closely related to *B. alpaminae* Gilg & Muschler, a Peruvian species which the former resembles greatly in leaf pubescence, ovary and fruit shape and pubescence, and style length. *Brayopsis gamosepala* is distinguished readily by its connate sepals that form a campanulate calyx and larger, only slightly biseriate seeds. In contrast, *B. alpaminae* has a polysepalous calyx and smaller (0.6–0.8 × 0.4–0.5 mm), typically biseriate seeds. The sepals in the latter species are often connivent, and during fruit maturity they, as in *B. gamosepala*, separate from the receptacle as a unit.

Although the development of a gamosepalous calyx in the Brassicaceae is now known in two species of unrelated genera, the feature alone does not justify the establishment of a new genus. In fact, had it not been for the gamosepalous calyx, *Brayopsis gamosepala* could have been easily mistaken for *B. alpaminae*. *Brayopsis* (six species) is a well-defined, monophyletic genus most closely related to *Eudema* Humb. & Bonpl. The taxonomy and the delimitation of the two genera

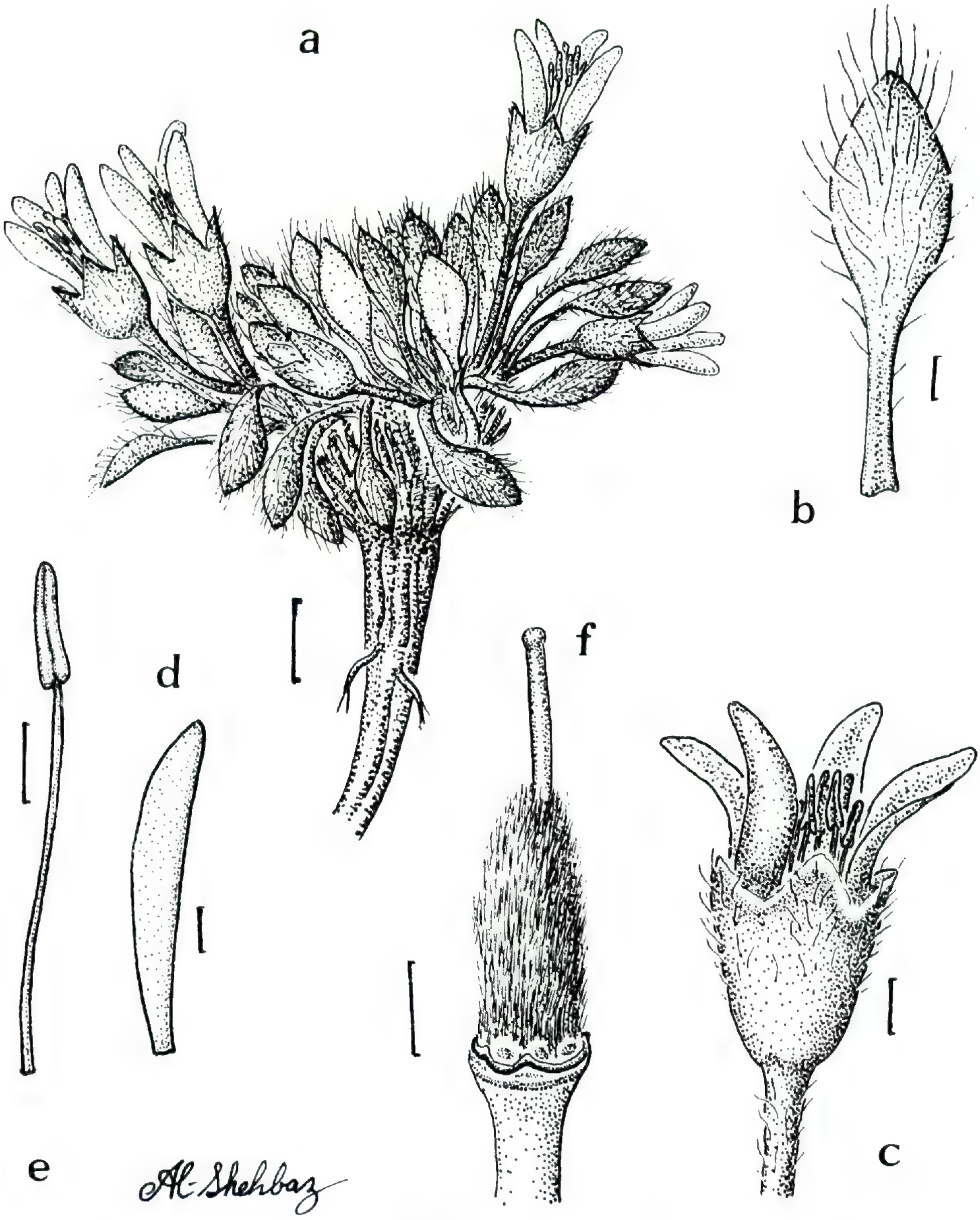

FIGURE 1. *Brayopsis gamosepala*.—a. Plant.—b. Leaf.—c. Flower.—d. Petal.—e. Stamen.—f. Pistil. Scales a = 4 mm; b–f = 1 mm. Drawn from the holotype.

have been recently treated (Al-Shehbaz, 1989, 1990).

I am grateful to Hannes Hertel, the director of Botanische Staatssammlung, München, for permitting the deposition of a few rosettes of the type collection at MO and GH. I am also thankful to George K. Rogers for his critical review of the manuscript.

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A NEW SPECIES OF *POLYPODIUM* (POLYPODIACEAE) AND TWO NEW SPECIES OF *HYPOLEPIS* (DENNSTAEDTIACEAE) FROM MESOAMERICA

The following new species are here described as a result of my work on the pteridophyte volume for the Flora Mesoamericana project.

Polypodium alansmithii R. C. Moran, sp. nov.

TYPE: Mexico. Chiapas: 22 km from San Cristóbal de las Casas on the road to Tenejapa, then right 3 km on the road to Matzam, 2,400 m, *Huft et al. 2173* (holotype, MO; isotype, UC not seen). Figure 1.

Rhizoma 2–4 mm latum latissime repens, squamis 2–4 mm longis bicoloribus lineari-lanceolatis adpressis; petiolis laminas circa aequantibus atrobrunneis; laminis (7–)10–18(–22) × 4.5–15 cm deltatis lanceolatis vel oblongis pinnatisectis vel pinnatis in parte basale; pinnis 3–6(–8) mm latis integris vel raro crenatis, 8–16 utroque rhachidis latere.

Epiphytic, rarely epipetric or terrestrial; rhizome 2–4 mm wide, long-creeping, the scales 2–4 mm, lanceolate, bicolorous, black medially with pale brown margins, clathrate or subclathrate medially, appressed, denticulate to erose; petiole ca. equaling the lamina, dark brown, nonalate; lamina (7–)10–18(–22) × 4.5–15 cm, broadly deltate to broadly oblong, pinnatisect, sparsely scaly on both surfaces, the scales usually circular or ovate, occasionally with an acicular apex, subentire to denticulate; pinnae 2.5–8 × 0.3–0.6(–0.8) cm, pairs 8–16, entire to crenate, the distal ones ascending; veins free, obscure; sori round, not embossed adaxially.

Selected specimens examined. MEXICO. CHIAPAS: 11 mi. W of San Cristóbal Las Casas, along Hwy. 190, 2,350 m, *Croat 40499* (MO). OAXACA: along Hwy. 175 through Sierra de Juárez, 36.9 mi. S of bridge at Valle Nacional, ca. 0.5 mi. E of the Summit, 2,750 m, *Croat 48161* (MO); Dtto. de Mixe, Mpio. de Tontontepec, ca. 1 km N of road between Ayutla and Totontepec on turnoff to Villa Alta, 2,560 m, *Gereau et al. 2098* (MO). GUATEMALA. BAJA VERAPAZ: along dirt road 4 mi. NE of Purulhá, 1,500 m, *Croat 41287* (MO). TOTONICAPÁN: cloud forest of María Tecún, *Molina R. et al. 30394* (MO). HONDURAS. COPÁN: Quebrada La Hondura, 2 km NE de Santa Rosa de Copán, 1,000 m, *Mejía 43* (MO). FRANCISCO MORAZÁN: along road to Parque Nacional La Tigra, 22–25 km NE of Tegucigalpa, 1,850–2,125 m, *Croat & Hannon 63996* (MO); above Rosario Mine, San Juancito Mts., 1,800 m, *Morton 7417* (MO); La Tigra, 1,600 m, *Regina A. 32* (MO). INTIBUCÁ; Cerro San Cristóbal, La Esperanza, 2,000 m, *Mejía O. 100* (MO). EL SALVADOR. SANTA ANA: Cerro Verde, 1,900 m, *Siu s.n.* (MO). SONSONATE: Cerro Verde cloud forest, 2,000 m, *Seiler 1474* (MO). NICARAGUA. ESTELÍ: Cumbre del Cerro Quiabú, 7 km W de Estelí, 1,600 m, *Neill 1225* (MO). MADRIZ: Cerro Pataste, ca. 20 km SW de Ciudad Somoto, 1,700 m, *Grijalva 913* (MO). JINOTEGA: along Hwy. 3, ca. 1 km NW of La Fundadora entrance, unnamed peak ca. 500 m W of hwy., 1,450–1,520 m, *Stevens 20369* (MO); carretera Matagalpa–Jinotega, La Fundadora, 1,400 m, *Moreno 1865* (MO). MATAGALPA: El Arenal, 500 m sigiendo el camino de Aranjuez, 1,400 m, *Moreno 9590* (MO); Fuente Pura, km 142, carretera Matagalpa–Jinotega, 1,400–1,450 m, *Moreno 16997* (MO).

This species is named for Alan R. Smith (UC), who has given me much help and encouragement with the Flora Mesoamericana project. The species occurs from southern Mexico (Guerrero, Oaxaca, and Chiapas) to Nicaragua, from 1,500 to 3,600 m. In the Floras of the region, it has previously been included in *P. montigenum*, which is closely related but differs by the characteristics given in the following key:

1. Lamina (12–)22–35(–50) × (4–)14–18 cm, 1-pinnate throughout; pinnae 7–15 mm wide, pairs 11–21, the distal ones perpendicular to the rachis or nearly so; petiole ½–¾ the length of the lamina; Costa Rica, Panama ..... *Polypodium montigenum*

1a. Lamina (7–)10–18(–22) × 4.5–15 cm, pinnatisect throughout or 1-pinnate basally; pinnae 3–6(–8) mm wide, pairs 8–16, the distal ones ascending; petiole ca. equaling the length of the lamina; southern Mexico to Nicaragua ..... *Polypodium alansmithii*

Since most of the distinguishing characteristics deal with leaf size and dissection, it could be argued that *Polypodium alansmithii* is merely a smaller, less-cut version of *P. montigenum*. The two com-

a
b
c
d
15 cm
f
g

pletely differ in range, however, which supports their separation. Actually, *P. montigenum* is most closely related to *P. plebeium* Schldl. & Cham., which occurs from Mexico to Panama. *Polypodium montigenum* differs from *P. plebeium* only by its appressed, rather than spreading, rhizome scales.

Polypodium montigenum is redescribed below with a list of specimens examined because it has been too broadly circumscribed in the past. It is endemic to the mountains of Costa Rica and Panama, where it grows in cloud forests from 1,800 to 3,100 m.

Polypodium montigenum Maxon, Publ. Field Mus. Nat. Hist., Bot. Ser. 17: 306. 1938. TYPE: Costa Rica. Heredia: along the cart road from Vara Blanca (between Poás and Barba volcanoes) to La Concordia, 1,600–1,950 m, *Maxon & Harvey 8479* (holotype, US; isotype, NY not seen). Figure 2.

Epiphytic on tree trunks or clambering on surrounding vegetation; rhizome 3–6 mm wide, long-creeping, the scales 2–5 mm, linear-lanceolate, bicolorous, black or dark brown medially with narrow whitish margins, not clathrate medially, appressed, fimbriate to erose; petioles ½–¾ as long as the lamina, dark brown, nonalate; lamina (12–)22–35(–50) × (4–)14–18 cm, lanceolate to narrowly oblong, 1-pinnate throughout, sparsely scaly abaxially, the scales circular to ovate, sometimes with an acicular apex, ciliate; pinnae (2.5–)7–10 × (0.3–)0.7–1.5 cm, pairs 11–21, entire or crenate or (in large leaves) serrate, the distal ones perpendicular to the rachis or nearly so; veins free, obscure or rarely visible; sori round, not embossed adaxially.

Additional specimens examined. COSTA RICA. ALAJUELA: Angel Falls on road to Puerto Viejo, 5 km N of Vara Blanca, *Mickel 3575* (NY, UC). CARTAGO–SAN JOSÉ: Interamerican Hwy., vic. of Villa Mills and 1 km NW (vic. of Hotel La Georgina), 2,800–2,900 m, *Mickel 2181* (NY). CARTAGO: SE slope of Cerro de la Muerte, Cordillera de Talamanca, disturbed primary forest along Interamerican Hwy. 2,700 m, 23 May 1976, *Croat 35402* (MO). HEREDIA: SW, W, and N slopes of Volcán Barva, along road from Sacremento to Colonia Jesús María, 2,650–2,810 m, *Grayum 7484* (MO, NY, UC); Finca La Georgina y Vara Blanca, 1,950 m, *Jiménez 2074* (NY); Cerro Chompipe, N de San Rafael, 2,000 m, *Lems 6402829* (NY); 1 km W of Vara Blanca on the slope of Volcán Poás, 1,800 m, *Mickel 2501* (NY); Vara Blanca de Sarapiquí, N slope of Central Cordillera, between Poás and Barba volcanoes, 1,800 m, *Skutch 3513* (MO, NY). SAN JOSÉ: road from Cartago to San Isidro del General (Pan American Hyw., Rt. 2), between km 72 and 73, or 21–22 km SE of El Empalme, cloud forest, 2,750 m, *A. R. Smith & Béliz 1998* (MO, UC); along Interamerican Hwy., Cerro de la Muerte, 3,100 m, *Hennipman et al. 7124* (MO); S of Cartago, ca. 4 km S of El Empalme near La Chonta, 2,500 m, *Lellinger 1580* (MO). PANAMA. CHIRIQUÍ: Guadalupe–Cerro Punta, Finca J. L. Caballero, 1 km de la carretera principal, 2,000 m, *Caballero 95* (MO); Las Nubes, 5.5 km NW of Río Chiriquí Viejo, W of Cerro Punta, 2,200 m, *Busey 672* (MO); Distrito Bugaba, Cerro Punta, 8°52′N, 82°33′E, cloud forest, 2,200 m, *van der Werff & Herrera 6273* (MO, UC).

The labels on several specimens (e.g., *Smith & Béliz 1998*) state that the rhizome is scandent on surrounding vegetation, not clinging to trees. As far as I know, this growth habit has not been previously recorded in *Polypodium*. Other labels, however, state that the plants were growing as epiphytes on tree trunks.

Hypolepis trichobacilliformis R. C. Moran, sp. nov. TYPE: Panama. Chiriquí: along trail between N fork of Río Palo Alto and Cerro Pate Macho, ca. 6 km NE of Boquete, 8°48′N, 82°23.5′W, 1,600–2,000 m, 6 Feb. 1986, *A. R. Smith et al. 2361* (holotype, MO; isotype, UC). Figure 3d–f.

Petiolus brunneus vel pallide brunneus spinosus; laminae utrinque pubescentes, pilis bacilliformibus plerumque adpressis pallide rubellis, margine glabris; indusiis viridibus saepe absentibus.

Leaves to ca. 1.5 m(?), continuous in growth, erect; petiole brown throughout or stramineous distally, epipetiolar branches present laterally near the base, usually 1–2; both surfaces of the lamina moderately pubescent along and between the veins with minute, mostly appressed, pale reddish, bacilliform hairs, lacking catenate hairs; lamina margins eciliate; costae of the penultimate segments not bordered adaxially by perpendicular, decurrent, herbaceous wings; rachis not spiny, brown to stramineous, straight (not flexuose) basally, glabrous; veins not ending in shallow emarginations; indusia ca. 0.1 mm wide, eciliate, green like the lamina or slightly scarious, not or only scarcely

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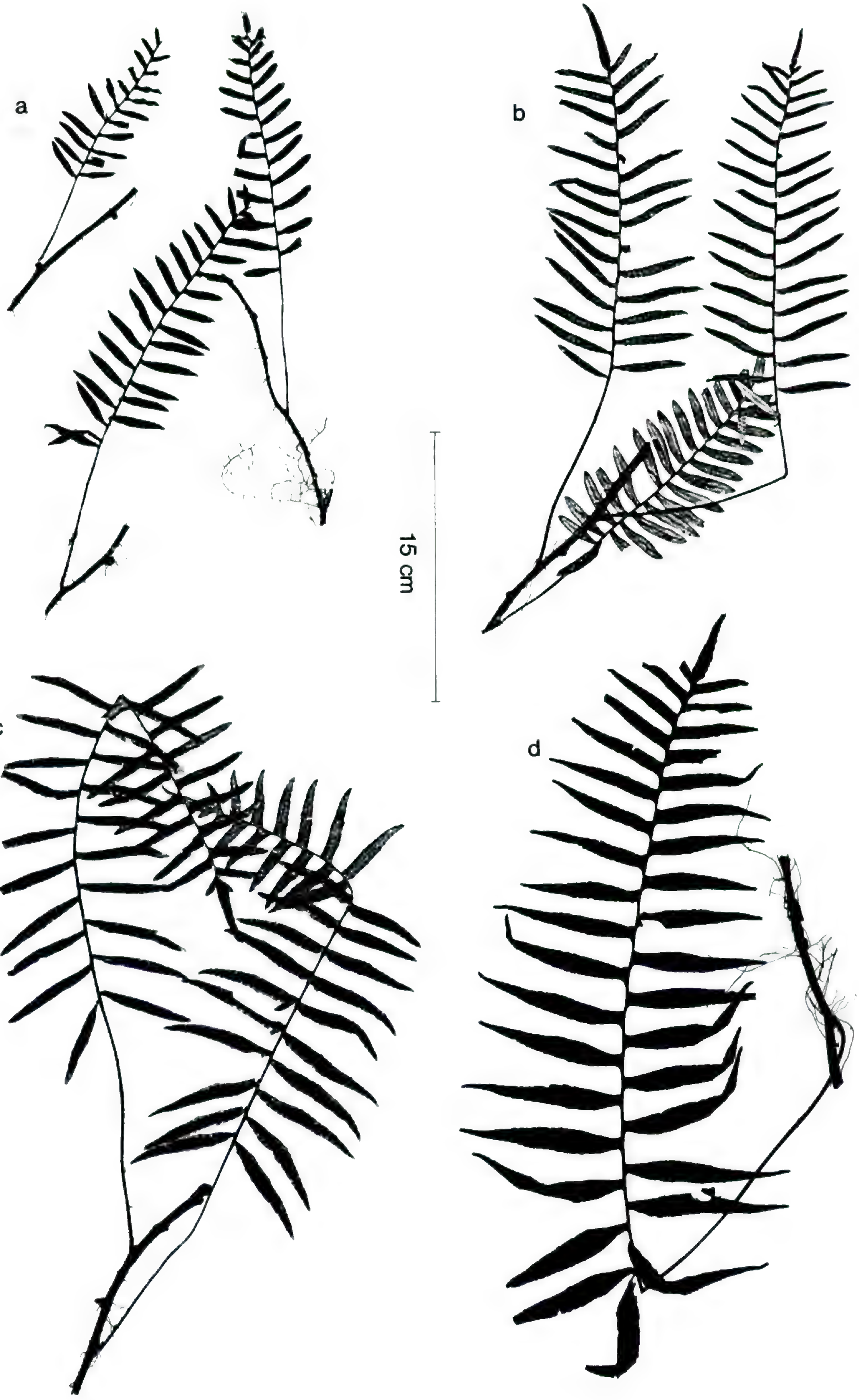
FIGURE 1. Fertile leaves of *Polypodium alansmithii*.—a. Honduras, *Mindence 31* (MO).—b. El Salvador, *Seiler 1474* (MO).—c. Honduras, *Espinal 55* (MO).—d. Guatemala, *Molina R. et al. 30394* (MO).—e. Honduras, *Mejia O. 100* (MO).—f. Honduras, *Clare 203* (MO).—g. Honduras, *Crúz P. 73* (MO).


a
b
15 cm
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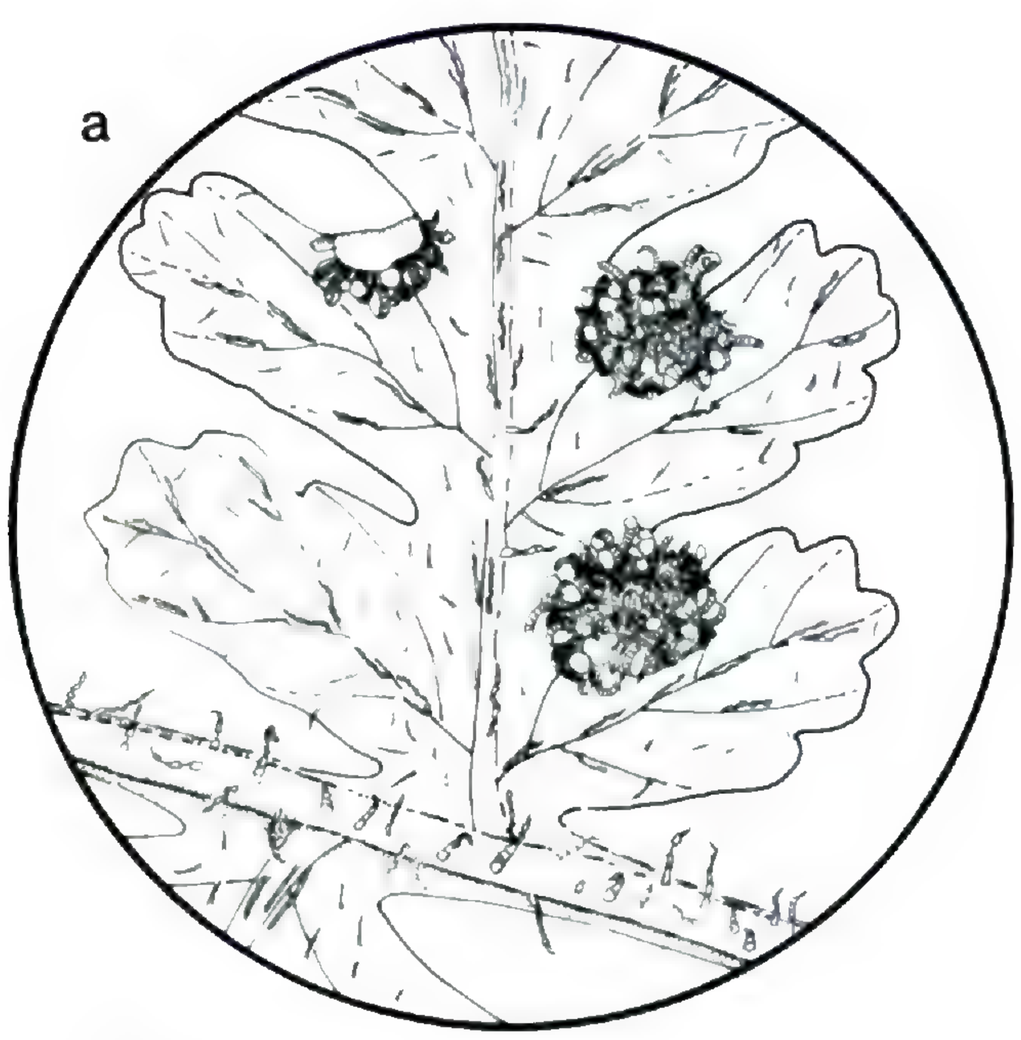
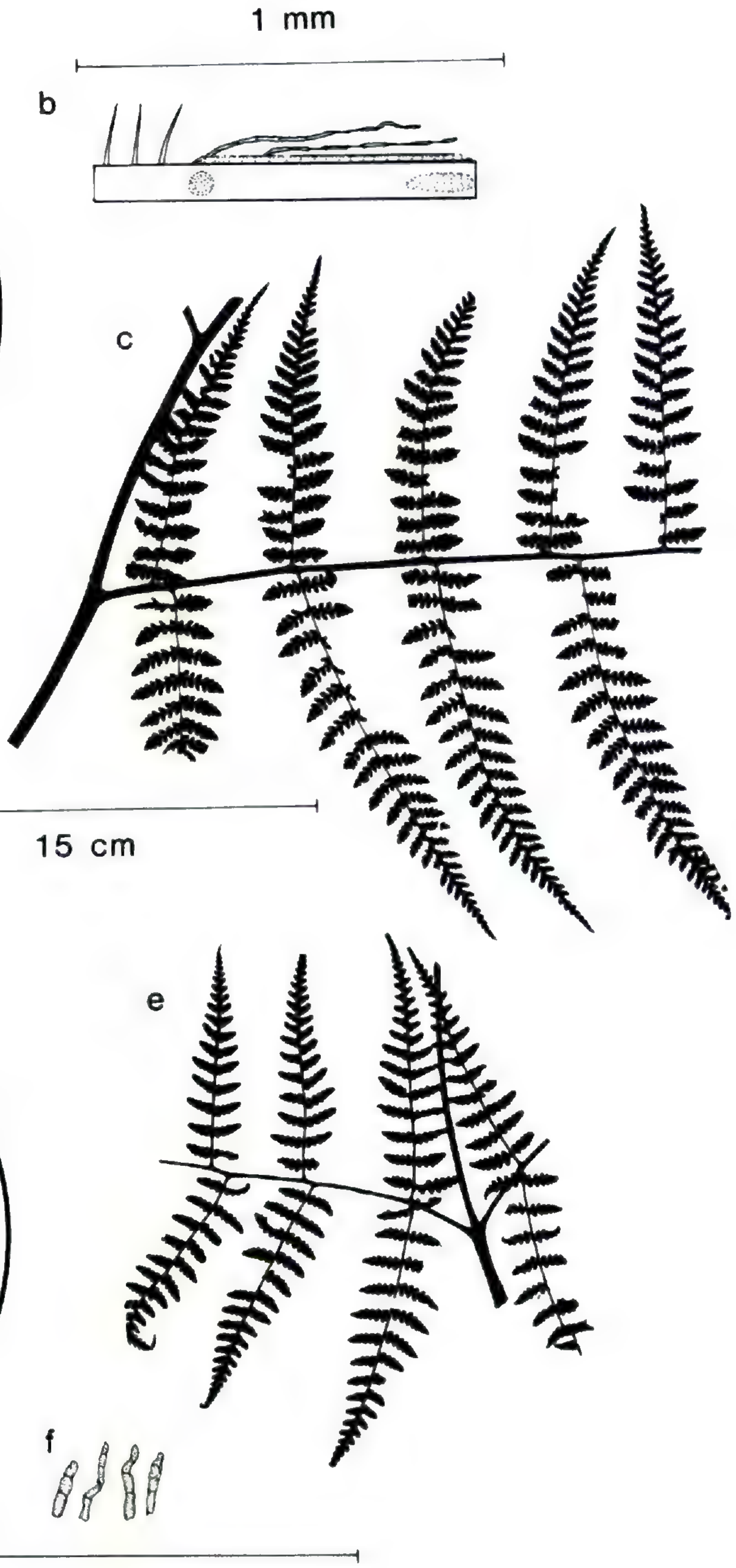
d





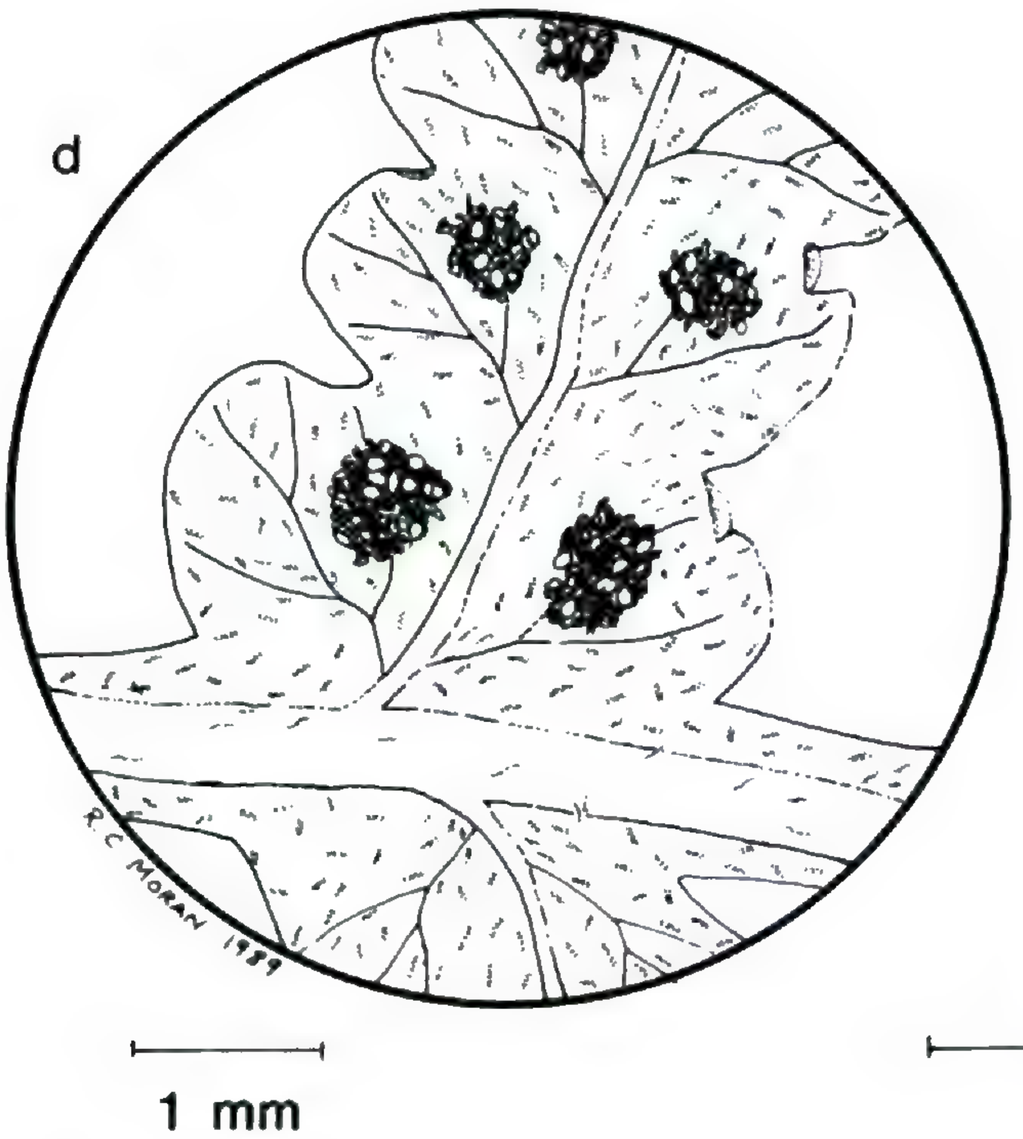


FIGURE 3. *Hypolepis ditrichomatis* (a–c) and *H. trichobacilliformis* (d–f).—a. Abaxial surface of tertiary segment.—b. Side view of acicular hyaline hairs between veins (left) and appressed reddish hairs along veins (right).—c. Basal portion of pinna.—d. Abaxial surface of tertiary segment.—e. Pinna bases.—f. Bacilliform hairs. a–c, *van der Werff & Herrera 6265* (MO). d, *Smith et al. 2361* (MO). e, f, *van der Werff & Herrera 6472* (UC).

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FIGURE 2. Fertile leaves of *Polypodium montigenum.*—a. Costa Rica, *Hennipman et al. 7124* (MO).—b. (Holotype) Costa Rica, *Maxon & Harvey 8497* (US).—c. Costa Rica, *Lellinger 1580* (MO).—d. Panama, *van der Werff & Herrera 6273* (MO).

reflexed and apparently absent, or fully reflexed but covering only ¼–½ of the sorus.

Additional specimens examined. COSTA RICA. ALAJUELA: Volcán Poás, *Stork 2507* (UC); Achiote, Volcán Poás, 2,200 m, *Tonduz 10696* (US). CARTAGO: Santa Clara de Cartago, 1,950 m, *Maxon & Harvey 8229* (US); Roble, massif de l'Irazu, 2,000 m, *Pittier 4173* (US). HEREDIA: Vara Blanca de Sarapiquí, N slope of Central Cordillera, between Poás and Barba volcanoes, 1,615 m, *Skutch 3600* (US). SAN JOSÉ: Cerro Chirripó, SW slopes along ridge trail from Canaan to summit, ca. 2,500 m, *Evans et al. 55* (US); Cerro de la Muerte, 1 km NW of Villa Mills on Interamerican Hwy., Hotel La Georgina, 2,900 m, *Lellinger 861* (US); Cerro de la Muerte, km 173 along the Interamerican Hwy., 2,600 m, *Mickel 3300* (US); Las Nubes, 1,500–1,900 m, *Standley 38807* (US); near Finca La Cima, above Los Lotes, N of El Copey, 2,100–2,400 m, *Standley 42695a* (US); on Pan American Hwy. above La Georgina, slopes of Cerro de la Muerte, 3,000 m, *Stone 2015* (DUKE). CARTAGO/SAN JOSÉ: ca. 3 km SE of Trinidad or 42 km SE of San Isidro de Cartago along the Carretera Interamericana, 2,600 m, *Wilbur 27801* (DUKE). PROVINCE UNKNOWN: San Geronimo, 1,500 m, *Wercklé 581* (US). PANAMA. CHIRIQUÍ: Distrito Bugaba, Cerro Punta, along ridge to watershed to Bocas del Toro, 8°52′N, 82°33′E, 2,200 m, *van der Werff & Herrera 6472* (MO, UC). CHIRIQUÍ/BOCAS DEL TORO: trail along the continental divide to ca. 3 km E of Cerro Pate Macho, cloud forest, 2,000–3,000 m, *Smith et al. 2442* (UC); trailside in Quebrada Bajo Grande ca. 2 mi. E of Cerro Punta, 2,300 m, *Wilbur et al. 13146* (DUKE).

This species grows in cloud forests, wet forests, clearings, and pastures from 1,600 to 2,200 m. It differs from all other *Hypolepis* in Mesoamerica by having short, cylindrical, bacilliform hairs on the lamina and medial sori that are not or only slightly protected by reflexed indusia. The density of the bacilliform hairs may vary from sparse to moderate, even on the same leaf. Larger catenate hairs, which occur on the abaxial surface in all other species of *Hypolepis* in Mesoamerica, are lacking in this species.

The indusia of *H. trichobacilliformis* are not or only slightly reflexed and texturally modified. In those cases where the indusia are fully reflexed, they cover ¼–½ of the sorus. Because the sori are naked or only partially covered, some specimens of this species have been named as *H. nuda* Mett. ex Kuhn, a species endemic to the Andes of Venezuela. *Hypolepis nuda* differs by its marginal sori that tend be elongated, short-stalked pinnae, and oval or semicircular segments.

Hypolepis ditrichomatis R. C. Moran, sp. nov. TYPE: Panama. Chiriquí: vicinity of Guadalupe, between Río Chiriquí Viejo and the continental divide, 8°53′N, 82°36′W, 2,200 m, *Churchill & de Nevers 5048* (holotype, MO—3 sheets). Figure 3a–c.

Petiolus brunneus vel pallide brunneus; laminae utrinque pubescentes, pilis erectis acicularibus hyalinis secus et inter venus praesentibus et pilis (fere) adpressis gracilibus pallide rubris solum secus venas praesentibus praeditae; margine ciliatae.

Leaves to ca. 2 m, continuous in growth, scandent; petiole brown to tan, spiny, sparsely pubescent to glabrescent; both surfaces of the lamina sparsely to moderately pubescent along and between the veins with two kinds of hair, the first erect, acicular, hyaline, and found throughout, the second appressed or nearly so, slender, pale reddish, and found only on the veins and costae; lamina margin eciliate; costae of the penultimate segments not bordered adaxially by a perpendicular herbaceous wing; rachis spiny, brown, tan, or stramineous, straight or only slightly flexuose basally, sparsely pubescent to glabrescent; veins not ending in shallow emarginations; indusia 0.2–0.3 mm wide, scarious, eciliate.

Additional specimens examined. COSTA RICA. ALAJUELA: slope of Volcán Poás at bridge just below Hacienda El Tirol, 2,000 m, *Mickel 2000* (UC). CARTAGO: Tapantí, ca. 15 km S of Paraíso, 1,150 m, *Mickel 2306* (US); along Interamerican Hwy. between Cartago and San Isidro de El General, *Scamman 7028* (GH, US, UC). HEREDIA: Vara Blanca, between Poás and Barba volcanoes, 1,600–1,700 m, *Maxon & Harvey 8303* (US); steep pastured slopes of Volcán Barba, ca. 4 km from Vara Blanca on the N slopes, 1,750 m, *Wilbur & Stone 10085* (DUKE, US). SAN JOSÉ: 25 km N of San Isidro de El General along the Interamerican Hwy., 1,800 m, *Burger & Liesner 7038* (F, GH); slopes of Cordillera Talamanca, near La División N of San Isidro de El General, 2,400–2,900 m, *Williams et al. 24425a* (F). PANAMA. CHIRIQUÍ: upper Caldera Watershed, above El Boquete, 1,650–1,925 m, *Maxon 5658* (US); Disto. Bugaba, Cerro Punta, cloud forest, 2,200 m, *van der Werff & Herrera 6260* (MO, UC), *6265* (GH, MO, UC, US); Guadalupe, Cerro Punta, finca Maduro, 2,000 m, *Caballero 120* (F, MO, PMA); Cerro Colorado, along road to copper mine 34.1 km beyond bridge over Río San Felix near town of San Felix, 13.1 km beyond turnoff to Escopeta, 1,390 m, *Croat 37306* (MO).

This species grows in cloud forests from 1,200 to 2,900 m. It can be distinguished from all other *Hypolepis* in Mesoamerica by the two kinds of hairs on the lamina (see description). The slender, pale reddish hairs along the axes and veins are similar to those in *H. parallelogramma* Kunze, a South American species. That species, however, lacks the short, erect, hyaline, acicular hairs found on *H. ditrichomatis* and has a different cutting of the lamina.

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A NECESSARY NEW COMBINATION IN *DUROIA* (RUBIACEAE)

A new combination in *Duroia* is required in anticipation of the forthcoming *Flora of the Venezuelan Guayana* (Steyermark & collaborators, in prep.) due to the earlier publication by Ladbrook (July 1920) of a specific epithet in *Coupoui*, *C. micrantha*. Ladbrook's epithet was treated by Steyermark (1965, 1974) as a synonym of *Duroia sprucei* Rusby (Dec. 1920). Unfortunately, Rusby's name must be replaced by the new combination proposed below. The July 1920 fascicle [No. 691] of the *Journal of Botany, British and Foreign*, which included Ladbrook's article, was date stamped by the Missouri Botanical Garden Library as received "JUL 21 1920." The date of issue of Rusby's work, as given on the cover and confirmed elsewhere (Stafleu & Cowan, 1983), is "December 20, 1920."

In the protologue of *D. sprucei*, Rusby (1920) cited *Rusby & Squires 171* and *172* and indicated that they are "the same as Spruce's 3624." Therefore, these three collections are syntypes of the name. Steyermark (1965) declared the "holotype" of *D. sprucei* to be the NY specimen of *Rusby & Squires 172* with isotypes at F and US, and the NY specimen of *Rusby & Squires 171* to be a syntype. Steyermark clearly meant to lectotypify *D. sprucei* because he identified *Rusby & Squires 171* as a syntype. Therefore, *Rusby & Squires 172* (NY) is the lectotype of *D. sprucei*, and duplicates of that collection (F, MO, US [3 sheets]) are its isolectotypes.

Steyermark labeled the NY specimen of *Rusby & Squires 171* as "holotype" of *D. sprucei* (IDC microfiche NY 972-C-4). Possibly there was an error in preparation of the manuscript or in publication causing the numbers *171* and *172* to be switched. The collection at US contains three duplicates of *Rusby & Squires 172* and no duplicate of *171* (D. Nicolson, pers. comm.). Therefore, in accordance with Steyermark's published statements, the numbers are correct as published. Steyermark either changed his mind after annotating *171* at NY, perhaps deciding at the last minute to use a specimen from the collection with more duplicates as the lectotype, or placed his annotation label on the wrong specimen by accident. The conclusions drawn herein do not conflict with Article 8 of the Code (Greuter et al., 1988).

Duroia micrantha (Ladbr.) Zarucchi & Kirkbride, comb. nov. Based on *Coupoui micrantha* Ladbr., J. Bot. 58(691): 176–177. 1920 [ante 21 July 1920]. TYPE: "Guiana," *Martin s.n.* (holotype, BM).

Duroia sprucei Rusby, Descr. S. Amer. Pl. 133. 1920 [20 Dec. 1920]. TYPES (Steyermark, 1965): Venezuela. Delta Amacuro: Sacupano, Apr. 1896 (fr), *Rusby & Squires 172* (lectotype, NY not seen; isolectotypes, F, MO, US-32553, US-1158548, US-1390424); *Rusby & Squires 171* (lectoparatype, NY not seen [IDC microfiche NY 972-C-4 with annotation as "Holotype"]); *Spruce 3624* (lectoparatypes not seen).

According to Steyermark (1974), the species is widely distributed in northern South America including the Río Orinoco drainage of Venezuela, the Rios Negro and Amazonas basins in Brazil, Colombia, and Peru, and Rupununi River in Guyana. Herbarium specimens also indicate its occurrence in Surinam. An excellent illustration of the species is given in Steyermark (1974, p. 691, fig. 109).

We thank Gerrit Davidse and Dan Nicolson for useful comments on the manuscript.

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A NEW CLOUD-FOREST *ERYNGIUM* FROM CHIAPAS, MEXICO

A new polyploid species, *Eryngium strotheri*, is described from the high-montane cloud forest of Chiapas, southern Mexico.

Eryngium strotheri Constance & Affolter, sp. nov. TYPE: Mexico. Chiapas: summit of Cerro Mozotal, E Sierra Madre, 15 Oct. 1980, *John L. Strother s.n.* (C-2189) (holotype, UC; isotypes to be distributed to principal herbaria). Figure 1.

Plantae crassae caulibus florentibus singularibus foliosis; folia virides non-disticha ± ensiformia lineari-lanceolata parallelo-nervata spinoso-lobata lobis cum spinula accessoria prominente munitis; inflorescentia viridis cymoso-

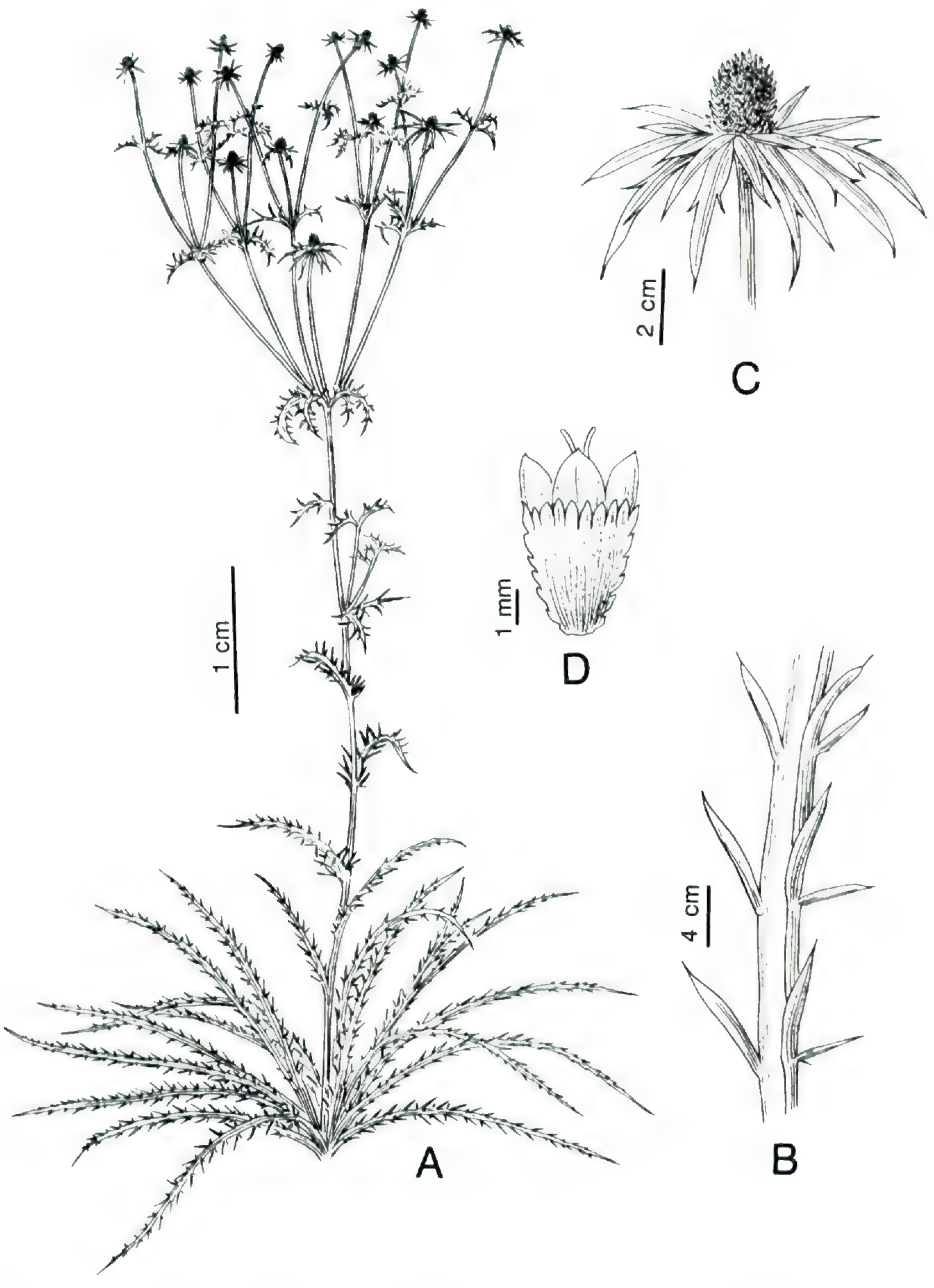

FIGURE 1. *Eryngium strotheri*.—A. Habit.—B. Detail of basal foliage leaf.—C. Head, with involucre.—D. External view of mericarp showing sepals and fruit squamae. (All from type collection.)

paniculata; capitula subnumerosa magna viridi-alba hemispherico-ovoidea glabra; bracteae involucrales distinctae biseriatae lateraliter imbricatae integrae vel spinoso-dentatae virides capitulo longiores; fructus cuneato-ovoideus squamatus alatus dorsi superficie nuda.

Plants perennial, stout, erect, 0.8–1.2 m tall, from a short vertical caudex bearing fascicled fibrous roots, the flowering stem solitary, leafy; basal leaves rosulate, spreading-ascending, nondistichous, ± ensiform, linear-lanceolate, 30–40 cm long, 2–5 cm broad (including lobes, 0.5–1 cm without lobes), densely spinose-lobed, the lobes linear to linear-lanceolate, spine-tipped, 1–2 cm long, spreading, mostly with an auxiliary axillary spinule, some as large as the lobes and giving a double-lobed appearance, the blade rigid-attenuate at apex, strongly caniculate, slightly tapering at base into a naked sheath no broader than the blade and 3–4 cm long, deep green, the venation strictly parallel except for veins entering the marginal lobes; cauline leaves similar to the basal, lanceolate to ovate, very coarsely and densely spinose-lobed with larger lobes, alternate below, whorled or opposite beneath the terminal inflorescence, subamplexicaul, spreading to reflexed; inflorescence paniculately cymose, ending in a large terminal cluster of ca. 5 basically trichotomous flowering branches surrounding and usually exeeding the terminal peduncle, without fertile axillary branches (?), conspicuously bracteate; heads greenish white, hemispheric-ovoid, 15–20 cm diam., pedunculate, many-flowered; involucral bracts 12–30, linear-lanceolate, 2.5–4.5 cm long, 2–7 mm broad, pungent, definitely in more than one series and imbricated laterally, entire or the larger outer ones with 2–5 spinose teeth, green on both surfaces, spreading, exceeding the heads; bractlets lanceolate-subulate, ca. 5 mm long, exceeding the fruit, a coma lacking; sepals broadly ovate, acute, apiculate, 1.5–2 mm long; petals oblong, ca. 1.5 mm long, the inflexed apex about equaling the limb, entire (?); styles 2–2.5 mm long, longer than the calyx; fruit cuneate ovoid, 4–5 mm long (including calyx lobes), 3 mm broad, compressed dorsally, provided with a row of flattened ovate-lanceolate scales below the calyx, the marginal wings lobed, the dorsal surface naked; chromosome number $n = 24$; cotyledons oval, 3–5 mm long.

Paratype. MEXICO. CHIAPAS: steep slope, evergreen cloud forest with *Quercus*, *Pinus*, *Abies*, *Drimys*, *Photinia*, *Clethra*, *Cornus*, and *Symplocus* on the N & W slopes of the Cerro Mozotal below the microwave tower along the road from Huixtla to El Porvenir and Siltepec, Mpio. Motozintla, 3,000 m, 28 June 1972, *D. E. Breedlove 25,829* (DS).

Clearly a member of sect. *Spinescentia*, *Eryngium strotheri* appears to combine the conspicuous involucre of *E. involucratum* Coult. & Rose with the branching inflorescence of *E. tzeltal* Constance and the foliage of *E. guatemalense* Hemsley. Indeed, the Strother material, which has been grown at Berkeley for seven years, was obtained in a generous attempt to fulfill the senior author's request for "seed" of *E. tzeltal*. The species of this group are all polyploid (4–9-ploid) so far as known and also strikingly variable. They may likely be capable of exchanging genes or even genomes at a polyploid level, which could account for the variability and their taxonomic complexity. The intricate interrelationships require further study in the field and garden.

The illustration was designed and executed by Charlotte Mentges Hannan.

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VALIDATION OF *CAESALPINIA* SUBGENUS *MEZONEURON* (DESF.) VIDAL AND NEW COMBINATIONS IN *CAESALPINIA* FOR TWO SPECIES OF *MEZONEURON* FROM AFRICA

While preparing a manuscript on fossil *Caesalpinia* (*Mezoneuron*) fruits from the Tertiary of North America (Herendeen & Dilcher, in press) it became apparent that new combinations in *Caesalpinia* have not been published for two *Mezoneuron* species from Africa. *Mezoneuron* Desf. was distinguished from *Caesalpinia* on the basis of its indehiscent winged fruits (Brenan, 1963; Hattink, 1974). However, *Mezoneuron* is now included in *Caesalpinia* due to similarities in floral and vegetative features (Hattink, 1974; Vidal & Hul Thol, 1976; Polhill & Vidal, 1981). New combinations in *Caesalpinia* have been published for the Asiatic species of *Mezoneuron* (Hattink, 1974; Vidal & Hul Thol, 1976). Vidal & Hul Thol (1976) regarded *Mezoneuron* as a subgenus of *Caesalpinia*; however, the subgeneric name was not validly published by these authors. This paper validates the name *C.* subg. *Mezoneuron* (Desf.) Vidal and establishes new combinations in *Caesalpinia* for two species of *Mezoneuron* from Africa.

Generic limits in the *Caesalpinia* complex have been difficult to define (Polhill & Vidal, 1981; G. P. Lewis, pers. comm.). Numerous genera were recognized by Britton & Rose (1930) based on carpological differences (Polhill & Vidal, 1981). Recent studies placing more emphasis on floral features have resulted in the abandonment of many of these segregate genera, including *Mezoneuron* (Gillis & Proctor, 1974; Hattink, 1974; Vidal & Hul Thol, 1976; Polhill & Vidal, 1981). Comparisons of leaflet epidermal anatomical features in *Mezoneuron* and 25 American and Asiatic *Caesalpinia* species, representing *Caesalpinia* sens. str. and six segregate genera recognized by Britton & Rose (1930), yield no significant differences between these groups (Herendeen, unpublished). These observations are consistent with those based on comparisons of floral and vegetative features. Subgeneric status for *Mezoneuron* is justified given the differences between these groups in fruit morphology.

Although the geographic distribution of *C.* subg. *Mezoneuron* is restricted today to Old World tropics and subtropics, paleobotanical evidence indicates that this group occurred widely across North America during the Tertiary (Herendeen, 1990; Herendeen & Dilcher, in press). The paleobotanical data demonstrate that *C.* subg. *Caesalpinia* and *C.* subg. *Mezoneuron* were distinct taxa by the Middle Eocene (Herendeen, 1990).

Caesalpinia L. subg. **Mezoneuron** (Desf.) Vidal ex Herendeen & Zarucchi, comb. et stat. nov. *Mezoneuron* Desf. Mem. Mus. Hist. Nat. 4: 245, t. 10, 11. (1818) (as *Mezonevron*). TYPE: *M. glabrum* Desf. = *C. pubescens* (Desf.) Hattink.

NEW COMBINATIONS

Caesalpinia L.

C. benthamiana (Baillon) Herendeen & Zarucchi, comb. nov. *Mezoneuron benthamianum* Baillon, Adansonia 6: 196 (1866). TYPE: Africa. Senegambia: *Heudelot s.n.* 1837 (holotype, P not seen).

Specimens examined. AFRICA. GUINEA: *J. G. Adams 3382* (MO, P, BARC-fruit). LIBERIA: *J. G. Adams 30186* (MO). NIGERIA: *R. C. Brown 923* (MO), *J. Opayemi s.n.*, 26 Nov. 1970 (MO). GHANA: *A. A. Enti 1637* (MO).

C. angolensis (Welw. ex Oliver) Herendeen & Zarucchi, comb. nov. *Mezoneuron angolense* Welw. ex Oliver, Fl. Trop. Afr. 2: 261 (1871). TYPE: Africa. Angola: *Welwitsch 606* (lectotype, LISU not seen; isolectotype, BM not seen).

Specimens examined. AFRICA. LIBERIA: *P. M. Danial 112* (MO). TANZANIA & KENYA: *O. Flock 552* (MO).

TANZANIA: *Harris et al. DSM 2621* (MO). UGANDA: *P. K. Rwaburindore 896* (MO), *P. K. Rwaburindore 1018* (MO). ANGOLA: *Welwitsch 607* (syntype, LISU not seen; isosyntypes, BM, K not seen).

Three species of *Mezoneuron* were recognized by Oliver (1871) from tropical Africa. In addition to the two species discussed above, *M. welwitschianum* Oliver was also described. This latter species was transferred to *Caesalpinia* by Brenan (1963) because the fruit is thickened along the placental suture, not winged as in other *Mezoneuron* species. Fruit morphology suggests that this species is not related to *C.* subg. *Mezoneuron*. Based on similarities in vegetative and reproductive morphology, Brenan (1963) suggested a relationship between *C. welwitschiana* and the Asiatic *C. tortuosa* Roxb.

Mezoneuron benthamianum and *M. angolense* were distinguished by Oliver (1871) on the basis of leaf size, and pinna and leaflet numbers:

Pinnae 5–6 pairs, leaflets 10–12 to each ..... *M. benthamianum*
Pinnae 8–10 pairs, leaflets 12–18 to each ..... *M. angolense*

Based on the specimens studied, it appears that these differences remain valid. In addition, differences between these species in details of leaflet epidermal anatomy further suggest that these are distinct species. Trichomes are more frequent on the abaxial epidermis of *C. benthamiana* than on *C. angolensis*, and cutinization of anticlinal walls of epidermal cells is less evident in *C. angolensis* than in *C. benthamiana*.

The authors thank the curators and staff of various herbaria (BARC, F, MO, US), which have made their collections available for ongoing studies of fossil and extant legumes. Special thanks go to C. R. Gunn and G. P. Lewis for constructive comments concerning this paper and the general problem of *Caesalpinia* delimitation. This work was supported in part by NSF Disssertation Grant BSR 88-00900 to PSH.

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CONCEVEIBA AUBLET (EUPHORBIACEAE) NEW TO AFRICA

The flora of tropical Africa is fairly well known, and in most areas botanical exploration produces few surprises. One exception is the Atlantic coastal forest of southern Cameroon and western Gabon, which is very rich in species and continues to yield new finds. The flora of this part of Africa has many links with that of South America; a common pattern is for a predominantly neotropical taxon (family, subfamily, tribe, or genus) to have a few representatives in central Africa (Thorne, 1973).

This paper describes an African addition to *Conceveiba* Aublet, a small neotropical genus of about nine species with its center of diversity in the Guianas (Jablonski, 1967). The African species is known only from mature forest in the Lopé Reserve in the Ogooué valley of central Gabon. The specimens were collected by J. M. and B. Reitsma from marked trees during a forest plot enumeration for the New York Botanical Garden.

The genus *Conceveiba* has been broadly defined by Jablonski (1967) to include two segregate genera, *Conceveibastrum* Pax & K. Hoffm. and *Veconcibea* Pax & K. Hoffm. He characterized the genus as having a trimerous ovary with three short styles, shortly connate at the base. The male flowers have numerous stamens, all fertile or with an inner ring of long, plicate staminodes.

The leaves, leaf arrangement, pistillate flowers, male inflorescence, male calyx, and individual stamens are all typical of the genus. Differences include the fruits, which are slightly lobed instead of trigonous or cylindrical, and the inflorescences, which are arranged monoeciously, while the rest of the genus is reportedly dioecious. *Conceveiba africana* also has distinctive male flowers. The number of stamens (7–10) is low for the genus, and the lack of an inner ring of staminodes distinguishes it from *Conceveiba* s. str. The presence of a pistillode in the male flowers is unique in the genus.

In view of the African material's strong overall affinities with Jablonski's genus, I do not consider the differences great enough to warrant the creation of a new genus. I am therefore including it in *Conceveiba* s.l. If the narrow view of *Conceveiba* were adopted, then a new genus to accommodate the African material would probably be needed. The combination of characters found in the new species is not seen in any one of the three narrow genera.

Conceveiba africana D. W. Thomas, sp. nov. TYPE: Gabon. Ogooué–Ivindo Province: Lopé Reserve, 0°30′S, 11°33′E, Chantier SOFORGA inventory, tree # 215, in mature forest, 27 Nov. 1986 (fl, fr), *J. M. & B. Reitsma 2618* (holotype, MO; isotypes, NY). Figure 1.

Arbores monoeciae ad 19 m altae. *Folia* coriacea dentibus glandulosis praedita morphologia respectu variantia: 1.8 ad 26 cm longa × 1.8 ad 14 cm lata in petiolis ad 10 cm longis; maioria elliptica basi acuta; minoria ovata basi subcordata in petiolis brevibus, glandulis duobus adaxialibus ad juncturam laminae petioloque notata. *Inflorescentiae masculinae* ramiflorae paniculatae ad 21 cm longae, ramis ad 5.5 cm; flores plerumque ternati, cymis contractis. *Flores masculini* calyce glabro quinquelobato fissuris ad dimidium extensis, staminibus filamentis longis glabris rectis vel vix plicatis, antheris quadricellularibus; pistillodium promineus pubescens. *Inflorescentia foeminea* racemo simplici terminale spiciforme notata crasso lignosoque in sicco costato squamis basalibus persistentibus praedita. *Flos foemineus* solitatius bractea lanceolata cum glandulis duabas basalibus subtentus; bracteolae duae saepe sine glandulis; calyx sepalis quinque sepalis liberis lanceolatis, 3–4 mm et stigmatibus tribus crassis rubris praedito, erectis tunc expansis ad 3.5 mm. *Fructus* glabrescentes, 1.1 cm longi, 1.7 cm diam., vix 3-lobati laeves in sicco protruberationibus planis praediti.

Medium-sized, much-branched, monoecious tree to 19 m tall, wood white, slash white and brittle, bark pale gray. Leaves coriaceous, 1.8–26 cm long, 1.8–14 cm wide, glabrous except for domatia, thinly pubescent when young; larger leaves alternate, elliptic, with an acute to obtuse base, the petiole terete, woody, articulated at both ends, to 10 cm long; smallest leaves clustered apically, ovate, with a rounded to subcordate base, the petiole thickened, 0.5–1.5 cm long; leaf margins thickened with glandular teeth; apex of both types acuminate; secondary nerves 5–14 on a side, departing at 45°–60° from the midrib, with a tuft of hairs in the abaxial axil. Male inflorescences yellowish and ramiflorous, from the axils of fallen leaves, forming pyramidal panicles to 21 × 11 cm, the dry rachis slender and ribbed, the lateral branches often with disc-shaped glands at the base. Cymes very contracted, often 3-flowered; first bract narrowly triangular, to 1 mm long, glabrescent; brac-

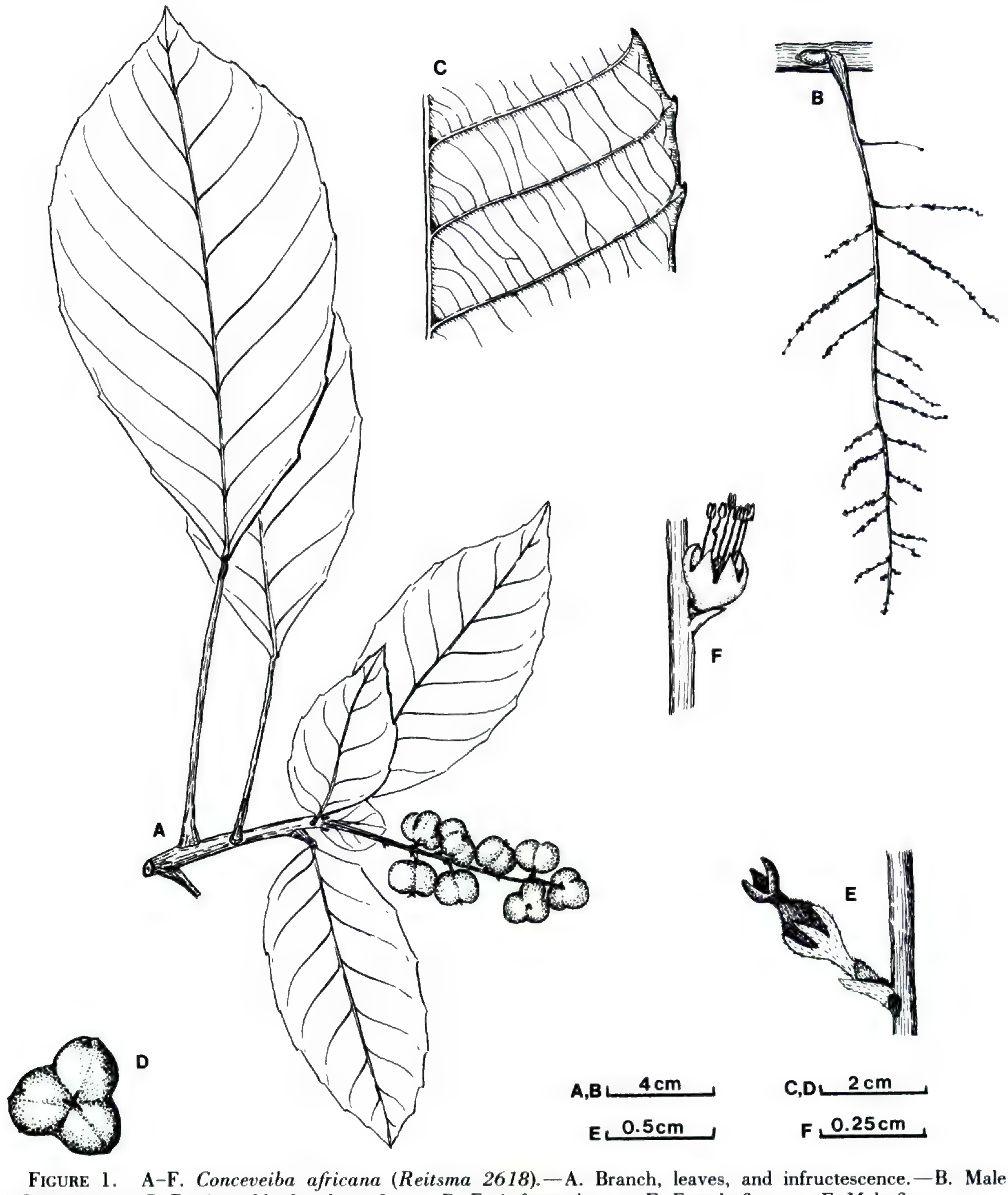

FIGURE 1. A–F. *Conceveiba africana* (*Reitsma 2618*).—A. Branch, leaves, and infructescence.—B. Male inflorescence.—C. Portion of leaf undersurface.—D. Fruit from above.—E. Female flower.—F. Male flower.

teoles and bracts of lateral flowers smaller and rounded, pubescent with spreading hairs. Flower buds rounded, apiculate, glabrous, 1 mm diam., the calyx valvate, closed. Male flowers apetalous, the calyx lobed to halfway with 5 triangular, acute sepals; stamens all fertile, 7–10 with long glabrous filaments, straight or slightly folded, anthers short, 4-celled, pubescent pistillode present. Female inflorescence a reddish, simple, terminal, spikelike raceme with basal triangular scales, ribbed when dry, shortly pubescent, 8–9 cm long; bracts 2–3 mm long, acute with 2 basal glands; bracteoles resembling bracts, with or without glands. Female flowers borne singly on short stout pedicels, apetalous, calyx open in bud, sepals 5, acute, 3–4 mm long, sometimes with a basal gland between two of them; ovary densely appressed-pubescent; stigma a stout column to 3 mm long with 3 stout styles to 3.5 mm, erect at first then spreading. Fruit glabrescent, dehiscent, shallowly 3-lobed, 1.1 cm

high, 1.7 cm diam., the surface smooth with occasional flattened protuberances in the dry state, style and sepals persistent, dehiscent, splitting into three 1-seeded portions leaving no column. Seeds about 0.9 cm long, smooth and brown with a conspicuous triangular hilum.

Additional specimen examined. GABON. OGOOUÉ-IVINDO PROVINCE: Lopé Reserve, Chantier LUFTEXFA, 0°30′S, 11°29′E, 30 May 1986 (female fl), *J. M. & B. Reitsma 2309* NY.

I thank John Dwyer for the Latin description, Mary Bucy for the illustration, and an anonymous reviewer for constructive comments. The study was supported by NSF grant BSR-88600682 to Duncan Thomas.

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A METHOD FOR COLLECTING DRIED PLANT SPECIMENS FOR DNA AND ISOZYME ANALYSES, AND THE RESULTS OF A FIELD TEST IN XINJIANG, CHINA

Dried and pressed plant specimens have been used for scientific study since the Italian Renaissance (Stafleu, 1971), and this remains the most common method of preserving the "information content" of living plants. Today, the standard herbarium specimen is routinely augmented by the preservation of material for anatomical, cytological, or chemical analysis (Davis & Heywood, 1963).

The growing application of molecular data in plant systematics requires methods for preserving material from which isozymes and nucleic acids can be recovered. In most cases, it has been considered necessary to transport plants quickly to the laboratory on ice, or to freeze and store plant tissues in liquid nitrogen until they can be returned to the laboratory. Both methods can be used quite successfully when the plants studied are nearby and in easily accessible localities. They have also been applied to collect material for molecular analysis in more remote regions (Sytsma & Schaal, 1985; P. Peterson, pers. comm.), but in these cases the logistics and the expense are prohibitive. In addition, the use of ice or liquid nitrogen storage is impractical when making large-scale "floristic" collections. An alternative to these methods seems most desirable.

The recovery of high molecular weight DNA from dried plant material has been demonstrated by Rogers & Bendich (1985) and Doyle & Dickson (1987). Pyle & Adams (1989) recently compared 27 treatments of plant specimens and found that only fresh, frozen, or dried plant tissues provided good yields of quality genomic DNA. They obtained high molecular weight DNA from spinach leaves following desiccation and storage in a desiccator for two months, but degradation was observed when tested at five months. These results prompted additional tests using both fresh and air-dried spinach placed directly into silica gel in jars. The initial results of this experiment are reported here.

The primary purpose of this report is to describe a field test of a simple and inexpensive drying method for preserving plant material for subsequent nucleic acid and isozyme recovery. This method is appropriate for use in remote regions and can easily complement the routine collection of herbarium specimens.

Materials and Methods

Preparation of plant material, DNA extraction, and gel electrophoresis of genomic DNA from fresh spinach (*Spinacia oleracea* L.) followed the protocol of Pyle & Adams (1989) with the following modification: Fresh and air-dried (42°C, 36 hr., in a plant press) leaves were placed directly in contact with silica gel, sealed in air-tight plastic bottles, and stored at 37°C for five months.

A field test was conducted during a 24-day expedition in the Xinjiang Uygur Autonomous Region, People's Republic of China. This remote region of northwestern China is characterized by a strongly continental climate. Collections were made in the Tarim Basin, Songarian Basin, and Tien Shan Mountains from sea level to 3,800 m. Approximately 2–5 grams of plant tissue were wrapped in tissue paper (to prevent plant tissue fragmentation) and placed in a 125-ml Nalgene bottle prefilled to one-third capacity with anhydrous $CaSO_4$, or Drierite (W. A. Hammond Co., Xenia, Ohio). Indicator Drierite was mixed with nonindicator Drierite in a 1 : 5 proportion. Bottles were labeled, tightly sealed, and stored at ambient temperature. Most plant tissue was completely dry within 24 hours. In succulent material a single change of Drierite was required.

Upon return to the laboratory, bottles were stored at −20°C. The hot CTAB procedure (Doyle & Dickson, 1987; Doyle & Doyle, 1987) was used to extract high molecular weight DNA. Best results were obtained when the dried plant material was ground in the presence of liquid nitrogen. Precipitation of DNA with isopropanol was carried out at −20°C overnight in order to increase yields. Restriction digests were carried out with the endonuclease *Hind* III for two hours at 37°C. Agarose-

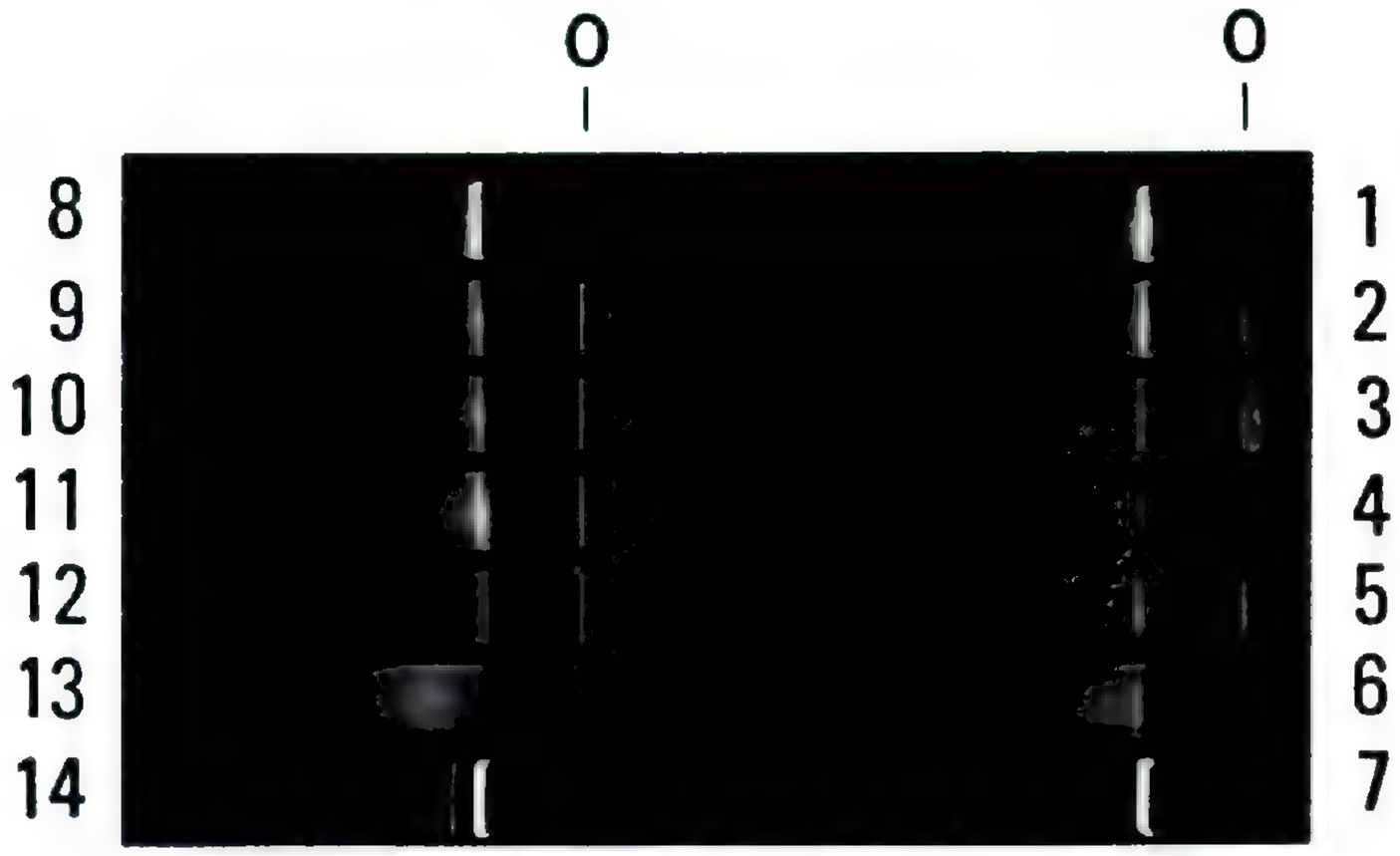

FIGURE 1. Comparison of spinach DNA from air-dried (lanes 2–6 for months 1–5) and fresh leaves stored on silica gel (lanes 9–13 for months 1–5). Lanes 1 and 8 are DNA from fresh spinach (control). Lanes 7 and 14 are lambda *Hind* III DNA markers. Size standards from the origin (O) are 23.1, 9.4, and 6.6 kb. The dual-loaded gel was run on agarose, 0.6%, 10 V/cm, 30 minutes.

gel electrophoresis and transfer of DNA from agarose gels to BioTrace (Gelman) nylon filters were conducted following standard protocols (Palmer, 1986). Preparation of digoxigenin-labeled probes, filter hybridizations, filter decolorization, and probe removal followed the manufacturer's instructions (Boehringer Mannheim Biochemicals; BMB) as modified by Rieseberg et al. (1990).

Chloroplast and nuclear ribosomal DNA variation was detected by hybridizing the filter-bound DNAs to plasmids containing a 9.9 kb *Sac* I fragment of the *Lactuca* chloroplast (courtesy of Rob-

TABLE 1. Taxa used for DNA extraction and isozyme analysis. Voucher specimens will be deposited in PEK and RSA. Collections are by Aaron Liston (L.) or James Morefield (M.). Specimens were used for successful DNA extraction (D), unsuccessful DNA extraction (X), isozyme analysis for ME, PGI, and TPI (I), and isozyme analysis for all enzymes used in unpublished studies of these genera (A).

Collection	Use		Family	Species
M. 5157	D		Asteraceae	*Artemesia dracunculus* L.
L. 827-12		I	Asteraceae	*Senecio krascheninnikovii* Schischk.
L. 829-5	D		Brassicaceae	*Lepidium latifolium* L.
M. 4993		I	Brassicaceae	*Lepidium latifolium* L.
M. 5042	D		Caryophyllaceae	*Cerastium beeringianum* Cham. & Schlecht.
L. 809-4	D	I	Chenopodiaceae	*Ceratoides latens* (Gmel.) Holmgren & Reveal
M. 5040	D		Crassulaceae	*Rhodiola coccinea* (Royle) A. Bor.
L. 819-7	D		Cyperaceae	*Carex* [sect. *Lamprochlaenae* (Drejer) Bailey] sp.
L. 816-1	D	A	Fabaceae	*Astragalus contortuplicatus* L.
L. 811-1	D	I	Fabaceae	*Glycyrhiza inflata* Batal.
L. 813-1		I	Fabaceae	*Sphaerophysa salsula* (Pall.) DC.
L. 819-3	D		Gentianaceae	*Gentiana aquatica* L.
L. 835-22	D	A	Paeoniaceae	*Paeonia anomala* L.
L. 823-8	D		Plantaginaceae	*Plantago minuta* Pall.
L. 808-9	D	I	Poaceae	*Aeluropus littoralis* (Willd.) Parl.
M. 4812	D		Primulaceae	*Glaux maritima* L.
L. 819-1		I	Ranunculaceae	*Thalictrum alpinum* L.
L. 818-24	D		Rosaceae	*Potentilla fruticosa* L.
M. 5067		I	Rosaceae	*Potentilla* aff. *pennsylvanica* Ledeb.
L. 821-2	X	I	Rosaceae	*Rosa platyacantha* Schrenk
L. 821-3		I	Rosaceae	*Rosa* sp.
L. 822-1		I	Rosaceae	*Rosa platyacantha* × *Rosa* sp.
M. 5200	D		Scrophulariaceae	*Lagotis integrifolia* (Willd.) Schischk.

ert Jansen) and a single 18S–25S rDNA repeat from *Helianthus argophyllus* Torr. & Gray (courtesy of Mike Arnold).

Sample preparation and enzyme electrophoresis followed the general methodology of Soltis et al. (1983). The tris-HCl grinding buffer-PVP solution described by Soltis et al. (1983) was used for enzyme extraction from dried plant tissue. All enzymes were resolved on 12% starch gels. The glycolytic enzymes malic enzyme (ME), phosphoglucoisomerase (PGI), and triosephosphate isomerase (TPI) were examined. A modification of gel and electrode buffer system 8 (Rieseberg & Soltis, 1987) was used to resolve these enzymes.

Results

Figure 1 shows genomic DNA from air-dried (lanes 2–6 for months 1–5) and fresh spinach (lanes 9–13 for months 1–5). Lanes 1 and 8 are DNA from fresh spinach (control). Lanes 7 and 14 are Lambda *Hind* III markers. Air-dried spinach DNA shows little change after four months storage at 37°C. However, the fresh spinach, placed directly in silica gel, sealed and stored at 37°C, always appears to be a little more degraded than air-dried and desiccated spinach. Both treatments appear to be degraded after five months storage.

Genomic DNA isolated from 15 species, representing 14 families, collected in China (Table 1) shows little or no degradation after four to six weeks of storage at ambient temperature (Fig. 2). Genomic DNA could not be successfully isolated from a species of the genus *Rosa* (Table 1). Figure 3 shows the results of hybridization of these same DNAs to the *Helianthus* 18S–25S rDNA repeat. Successful results were also obtained upon hybridization to the 9.9 kb *Sac1 Lactuca* chloroplast DNA probe (not shown).

Activity for the glycolytic enzymes PGI and TPI was obtained for 12 species representing eight families (Fig. 4). However, only two of these species (*Sphaerophysa salsula* and *Thalictrum alpinum*) had discernable activity for ME.

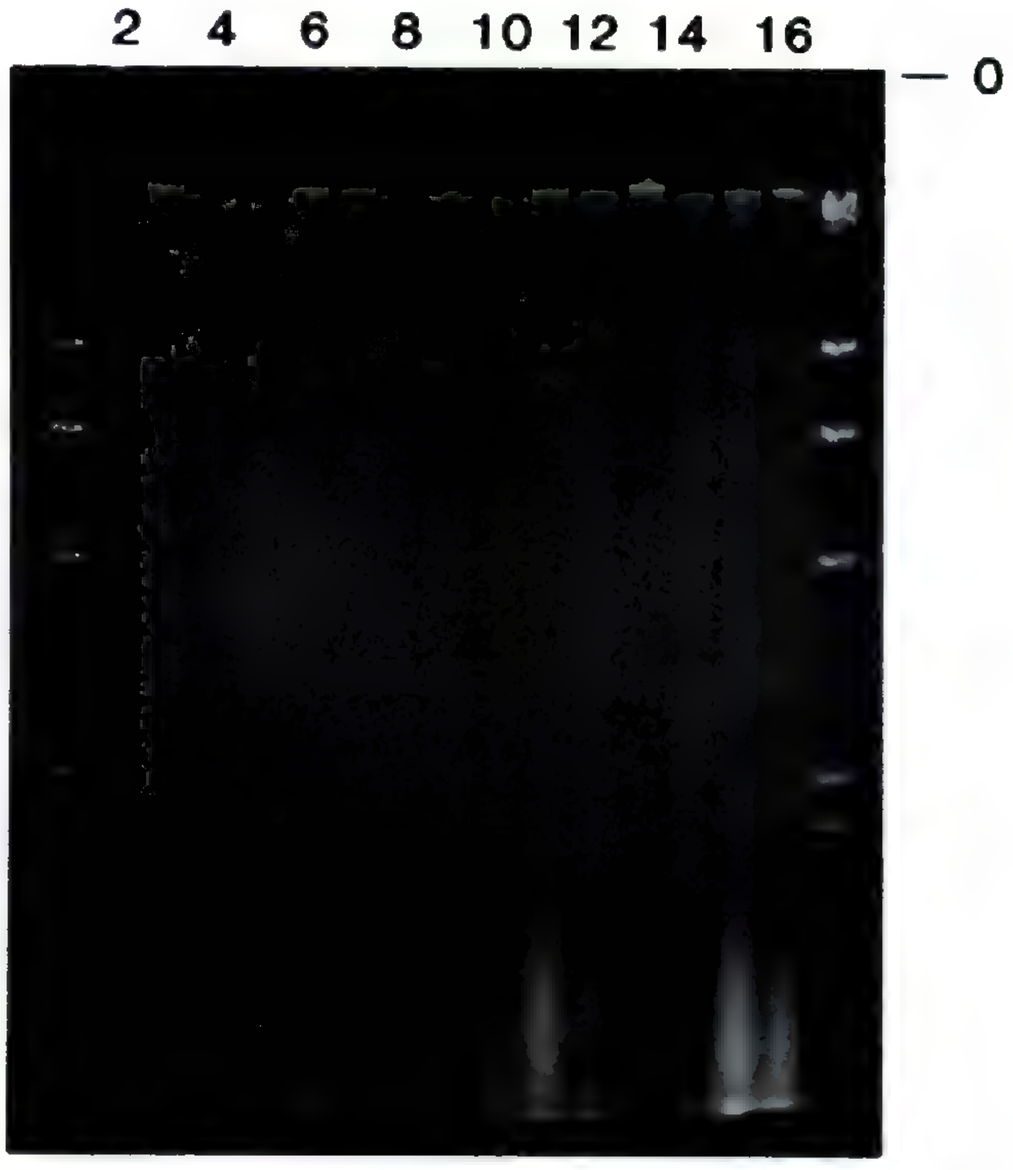

FIGURE 2. Undigested DNA from plants collected in Xinjiang, China, according to the described protocol. Lanes 1 and 17 are lambda *Hind* III DNA markers. Size standards from the origin (O) are 23.1, 9.4, 6.6, 4.4, 2.3, and 2.0 kb. The gel was run on agarose, 0.7%, 5 V/cm, 12 hours.—Lane 2. *Aeluropus littoralis.*—Lane 3. *Artemesia dracunculus.*—Lane 4. *Astragalus contortuplicatus.*—Lane 5. *Carex* sp.—Lane 6. *Cerastium beeringianum.*—Lane 7. *Ceratoides latens.*—Lane 8. *Gentiana aquatica.*—Lane 9. *Glaux maritima.*—Lane 10. *Glycyrhiza inflata.*—Lane 11. *Lagotis integrifolia.*—Lane 12. *Lepidium latifolium.*—Lane 13. *Paeonia anomala.*—Lane 14. *Plantago minuta.*—Lane 15. *Potentilla fruticosa.*—Lane 16. *Rhodiola coccinea.*

Discussion

The preservation of plant samples for DNA and isozyme analysis using only a drying agent and plastic bottles is simple, inexpensive, and of wide potential application. However, a few additional factors should be considered before the method is used in a particular study:

(1) Although genomic DNA was successfully isolated from 15 of 16 species examined, difficulty was encountered with the genus *Rosa*. Difficulties were initially found with material of the genus *Brongniartia* (Fabaceae) similarly collected in Mexico (O. Dorado, pers. comm.). It should be noted that DNA isolation from fresh material of these genera is also problematic due to the presence of polysaccharides, and alternative extraction procedures may be necessary.

(2) The examined species represented diverse growth forms including annuals, herbaceous perennials, succulents, and small shrubs. No trees were included in our study, but preliminary data from the genus *Arbutus* (Ericaceae) suggests that our technique can be used with woody taxa as well (Liston, unpublished). This technique has also been successfully used in recent collections of Ecuadoran Bromeliaceae (G. Brown, pers. comm.).

(3) Only three glycolytic enzymes were examined in the present study and no attempts were made to optimize the detection conditions for each species. In a preliminary analysis of 15 enzymes in the genera *Astragalus* and *Paeonia*, activity compa-

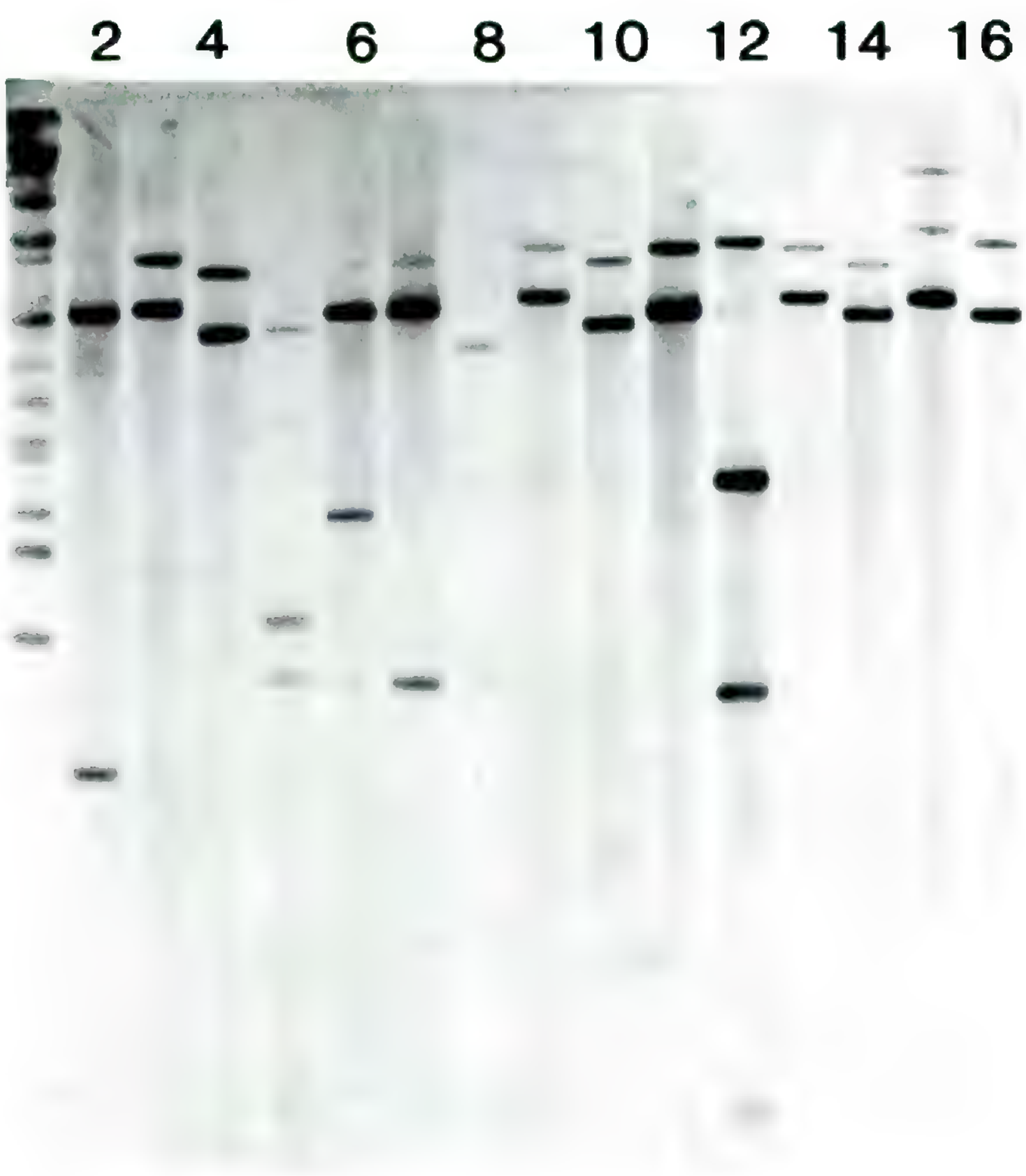

FIGURE 3. Southern blot of DNA from plants collected in Xinjiang, China, digested with *Hind* III and hybridized to a single 18S–25S rDNA repeat from *Helianthus argophyllus*. Lane 1 is lambda *EcoR* I, *Hind* III, *Sal* I, and *Sma* I DNA markers. Size standards (origin not shown) from the top of the gel are 32.7, 23.1, 21.2, 19.4, 15.3, 12.2, 9.4, 8.6, 8.3, 7.4, 6.7, 5.8, 5.6, 4.9, 4.4, and 3.5 kb. Lanes 2–16 are as in Figure 2.

rable to that of fresh material has been found in dried material of the Chinese species *A. contortuplicatus* and *P. anomala* (Liston & Zona, unpublished). Further study is needed to demonstrate the usefulness of this technique in actual isozyme studies.

In conclusion, we suggest that researchers interested in applying this technique to a particular taxon test the material beforehand, although our high rate of successful DNA isolation from a wide range of taxa suggests that it is worthwhile for any collector to obtain samples in this manner in ad-

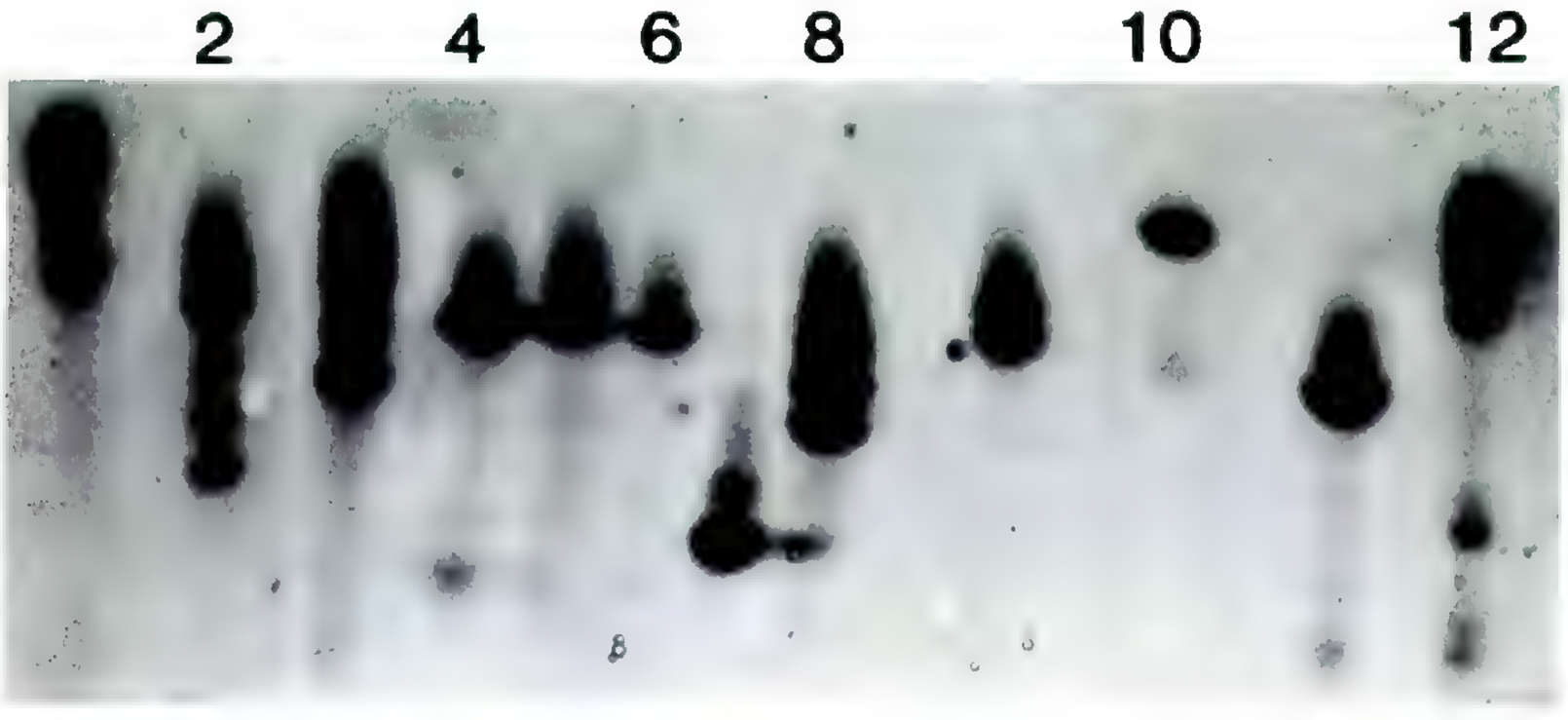

FIGURE 4. Enzyme activity for TPI from plants collected in Xinjiang, China, according to the described protocol.—Lane 1. *Aeluropus littoralis*.—Lane 2. *Ceratoides latens*.—Lane 3. *Glycyrhiza inflata*.—Lane 4. *Rosa platyacantha*.—Lane 5. *Rosa* sp.—Lane 6. *Rosa platyacantha* × *Rosa* sp.—Lane 7. *Paeonia anomala*.—Lane 8. *Sphaerophysa salsula*.—Lane 9. *Thalictrum alpinum*.—Lane 10. *Senecio kraschenninnikovii*.—Lane 11. *Potentilla* aff. *pennsylvanica*.—Lane 12. *Lepidium latifolium*.

dition to herbarium specimens. We also recommend that DNA extraction and isozyme analysis be carried out as soon as possible after reaching an appropriate laboratory, because studies with spinach indicate the possibility of degradation after several months of storage. Alternatively, samples can be frozen for long-term storage.

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BOOK REVIEW

Tan, Kit (editor). 1989. Plant Taxonomy, Phytogeography and Related Subjects: The Davis and Hedge Festschrift. Edinburgh University Press, 22 George Square, Edinburgh EH8 9LF, Scotland. Distributed in North America by Columbia University Press. xxvi + 351 pp. Hardbound. Retail price: 47.50 pounds.

This volume, commemorating a seventieth and a sixtieth birthday respectively, is one of those delightful books with which it must be so pleasant to have been associated, whether as editor or author. Peter Davis and Ian Hedge are, to quote the forward, ". . . two of the outstanding Edinburgh botanists of the latter half of this century." The contributors to the festschrift are from 25 institutes in 15 countries, and their contributions highlight current taxonomic problems, especially in the Mediterranean and southwest Asian regions so beloved by Davis and Hedge.

The 26-page preface contains brief biographical sketches, photographs, and extensive lists of the publications of the two celebrated botanists. The actual papers in this volume are a mixed bag and should include something of interest to almost everyone. New taxa of *Filago* and *Cichorium* (Compositae), *Bupleurum* and *Stoibrax* (Umbelliferae), *Grimmia* (Musci), *Veronica* (Scrophulariaceae), *Astragalus* (Leguminosae–Papilionoideae), *Iris* (Iridaceae), *Galium* (Rubiaceae), *Piptatherum* and *Stipa* (Gramineae), and *Peristylus* (Orchidaceae) are described. There are also revisions of *Monochoria* and parts of *Iris* and *Olea*.

The phytogeography papers are representative of the old school of geography; those biologists interested in vicariance biogeography will look in vain. One-seventh of the nearly 5,000 species of vascular plants in Greece are endemic. Arne Strid gives examples of these in relation to phytogeography and conservation. Another paper discusses floristic links and endemism in the Armenian highlands.

Rupert Barneby discusses some problems and consequences of typification in *Mimosa* in his usual eloquent fashion. A second paper by Barneby describes the identification of an object dug from the site of a former English bakery as a mesocarp of a menispermaceous genus that probably arrived on the site as a foreign body in a sack of Brazil nuts.

Two recurrent problems also reappear in the volume. The systematic position of *Rhabdodendron* is discussed in light of new and extensive embryological information. Although authors Tobe and Raven would place the genus in the Rosiflorae (but not in Dahlgren's Rosales), the mostly plesiomorphic embryological characters allow the actual placement of the genus to remain enigmatic. Of interest to a wider audience of botanists will be the chapter by Gertrud Dahlgren entitled "The Last Dahlgrenogram, System of Classification of the Dicotyledons." Published by his widow, this modified bubble diagram represents Rolf Dahlgren's last work on this topic before his fatal traffic accident in February 1987. A list of families and orders, as well as a discussion of the changes between this and the 1980 scheme, is given. Interestingly, the endings '-florae' for superorders have now been changed to '-anae'.

Finally, two light but enjoyable papers round out the volume. Plantsmen & Pottery discusses, among other things, Peter Davis's interest in the Scottish pottery known as Wemyss ware, slotting him among former and living biologists with close ceramic ties. The difficulties met on ten botanical expeditions to Iraq, Iran, Afghanistan and Pakistan over a period of 40 years are described in almost 50 pages by K. H. Rechinger. Air-travel is noticeable by its absence, as are the political problems and fighting, which now prohibit most travel to these areas. Almost 60,000 numbers were collected despite the perils and problems encountered. I recommend this account of recent travel in these areas, which have now largely changed forever.

Altogether, this is a most interesting and worthwhile compilation of papers, and it belongs on the shelves of most botanical libraries.—P. Mick Richardson, *Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.*

ERRATUM FOR *CAMPYLONEURUM NITIDISSIMUM* var. *ABRUPTUM*

An error in the comparison between *Campyloneurum nitidissimum* var. *abruptum* (Lindman) León and *C. coarctatum* (Kunze) Fée gives the exact opposite of the concept intended. The faulty sentence reads: "It is usually misidentified in herbaria as *C. coarctatum* (Kunze) Fée, from which it differs by its narrow, long-creeping stem, widely spaced phyllopodia, and leaves less than 40 cm long" (Ann. Missouri Bot. Gard. 77: 212). This should have read: "It is usually misidentified in herbaria as *C. coarctatum* (Kunze) Fée, **which differs by** its narrow, long creeping stem . . . . and leaves **more** than 40 cm long."

Campyloneurum coarctatum was described by Kunze in *Polypodium* based on material collected by Poeppig from Peru. The holotype was probably destroyed in Leipzig; however, there is other type material at Paris (P) and Vienna (W). I have seen both isotypes: at Paris there is a complete specimen with stem and leaf, while the specimen at Vienna (photo, BM) has only the leaf. Kunze applied the name to a plant with narrow (2–3 mm), long-creeping stems, well-spaced phyllopodia, elliptic to ovate-elliptic leaves with narrowly to abruptly cuneate bases, and undivided primary areoles. This name represents a well-defined species, which occurs from Costa Rica (León, Flora Mesoamericana, in press) to Bolivia, usually as an epiphyte. Thus *C. coarctatum* as here defined belongs to the *C. sphenodes* complex with long-creeping stems, well-spaced phyllopodia, and mainly undivided primary areoles, a group not closely related to *C. nitidissimum*.

Campyloneurum nitidissimum var. *abruptum* was described by Lindman as a variety of *Polypodium repens*, based on his own specimens collected during the Regnell expedition to Brazil. It is characterized by wide (5–10 mm), short-creeping stems, closely spaced phyllopodia, lanceolate to elliptic-lanceolate leaves, with attenuate to abruptly cuneate bases, and with or without divided primary areoles. Besides, it is only known from Colombia to Bolivia and Brazil, where it is commonly terrestrial.

The misunderstanding concerning the application of the name *C. coarctatum* for the species now recognized as *C. nitidissimum* var. *abruptum* was based on similarities of the leaf size and shape of base, which are characters of relatively little value.

—Blanca León, *Museo de Historia Natural, Av. Arenales 1256, Casilla 14-0434, Lima 14, Peru.*

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Books on Mosses from the Missouri Botanical Garden

Glossarium Polyglottum Bryologiae

A multilingual glossary for bryology
R. E. Magill, Editor
297 pp. 1990. $12.00.

This polyglot glossary provides definitions for nearly 1,200 terms in four languages—English, German, French, and Spanish. In addition, all English terms are translated into Japanese, Latin, and Russian.

The English vocabulary forms the core of the work, with each entry defined and cross-referenced to similar entries in the French, German, and Spanish glossaries, which also contain full definitions. The Japanese and Russian lists give translations of the English terms into these languages. The Latin vocabulary is essentially a translation of the English terms and indicates parts of speech and gender for all terms.

Cryptogamic Flora of the Yangtze Delta and Adjacent Regions

Hsu B.-s. (editor).
573 pp. + 28 plates. Text illustrations. 1989. $25.00.

In Chinese with Latin nomenclature. A special arrangement with the Shanghai Museum of Natural History makes this publication available at reduced cost. It treats about 1,100 species of algae, fungi (including lichens), bryophytes, and ferns.

Mosses of the Interior Highlands of North America

P. L. Redfearn, Jr.
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Treats about 300 species with family/genus key, generic descriptions, keys to species. Notes on habitats, occurrence, distribution.

Contributions to Systematic Bryology, dedicated to Lewis E. Anderson

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Flora of Southern Africa, Part 1 Mosses, Fascicles 1 and 2

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E. B. Bartram.
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Cover illustration. *Sisymbrium llatasii* Al-Shehbaz, by Ihsan A. Al-Shehbaz.